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CONTAMINANT LEVELS AND RELATIVE SENSITIVITIES TO CONTAMINATION IN THE DEEP-OCEAN COMMUNITIES

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INTRODUCTION

Recent changes in public policy presage increased dumping of sewage and other wastes on both East and West Coasts of the United States. On the East Coast there are an increased number of small and large municipalities that may seek ocean dumping permits (from Maine to Florida) and there is pressure to move dumping activities from inshore (e.g., the 12 mile site in the New York Bight) to deeper waters (the 106 mile Ocean Waste Disposal Site). On the West Coast there are an increased number of cities dumping (from small communities in Alaska to San Diego), and a potential shift from the current method of discharge of diluted sewage through ocean outfalls, to some ocean dumping of sewage sludge, perhaps into deep hypoxic basins. Leasing of outer continental shelf tracts for oil and gas exploration and proposed manganese nodule mining activities also increase the probability that other anthropogenic disturbances are likely to impinge on deep-sea communities. On both coasts the need is to determine the potential inpact of man's activities on these communities. Although some studies would suggest that the similarity in, for example, the PCB content of deep-sea organisms and those from coastal areas (excepting certain PCB hotspots) is due primarily to atmospheric input (Harvey and Steinhauer, 1976a,b), in other cases input from coastal areas to the deep sea may already be involved (Arima et al., 1979; Williams and Holden, 1973). Morover, evidence continues to accumulate on a variety of routes by which particle bound pollutants can rapidly reach the ocean floor, for example via fecal pellets produced by surface dwelling zooplankton, and mucous aggregates of biogenic and clay particles produced by coccolithophorids. Deuser et al. (1981) showed that fluxes of organic matter to the sea floor off Bermuda (3200 m) were closely tied to the annual cycle of primary production and more rapid than the 60-day resolving power of their study. Deuser (personal communication) has recently found evidence for the presence of fly ash particles in these deep ocean sediments, presumably originating from coal-fired power plants in the eastern United States.

The objectives of this study include documentation of the existing body burdens of contaminants in deep-sea fauna, and an assessment of the power that present knowledge of the biology of deep-sea communities gives us in predicting the outcome of increasing these levels of contamination.

Each of the four main sections of this report has separate authors, however, our conclusions and recommendations are a consensus based on our joint deliberations.

CONCLUSIONS

1. Deep-sea species diversity is extraordinarily high in comparison to the continental shelf. The deep sea may rival tropical rain forests in the number of undescribed species. The relative sensitivity of deep-sea communities cannot be predicted on the basis of their diversity alone.
2. Time to maturity (age at first reproduction) and number of offspring per clutch (brood size) are the most important determinants of population growth rates. Although there are few data, many or perhaps most deep-sea species have slow rates of population growth relative to continental shelf species. The ability to withstand disturbance (anthropogenic or otherwise) is related to rates of population increase (Section II).
3. Dispersal ability of deep-sea species remains poorly known and as many as half the species in major taxa with poor dispersal, such as the peracarids, may be endemic to ocean basins.
4. Physiological tolerances, metabolic rates and genetic variation are completely unknown in the highly diverse taxa most susceptible to local extinction.
5. The sensitivity of population growth rate to changes in demographic parameters depends on the structure of the life cycle. Some of the differences between deep-sea and shelf populations imply greater sensitivity in the deep sea; others imply the reverse. Thus no unambiguous prediction of deep-sea sensitivity can be made from the model presented.
6. In the absence of disturbance, the time required for local competitive extinction in the deep sea should be much longer than on the shelf.
7. Intermediate frequencies of disturbance can greatly extend the time required for local competitive extinction. The potential for this extension is greater in the deep sea, but deep-sea communities should also be more sensitive to exceeding the critical frequency. No unambiguous prediction of the overall relative sensitivity to disturbance can be made.

8. In spatially heterogeneous environments local diversity is maximized at intermediate disturbance frequencies. Longer competitive exclusion times and higher dispersal rates magnify this effect. Since deep-sea communities are characterized by longer local competitive extinction times, but lower dispersal rates, it is impossible to predict unambiguously their relative sensitivity to disturbance frequency.
9. Knowledge of body burdens of trace metals and organic pollutants in the deep-sea biota is very limited, but indicates that PCBs and DDT are present in livers of fish (rattails) from the continental slope of eastern North America in concentrations that may cause long-term deleterious effects.
10. The paucity of direct experiments on any aquatic species that relate body burdens of an organic contaminant to a specific adverse effect, and the fact that many current measurements of PCBs, DDT and PAHs in organisms do not identify the oxygenated metabolites of these compounds, render the correlations of the concentrations in the exposure habitat with observed effects relatively weak. Transferring these assumptions from coastal and shelf organisms to deep-sea biota, whose biology and biochemistry is less well understood, is therefore fraught with difficulty.
11. High resolution glass capillary gas chromatography and GC/MS data on organochlorines in deep-sea rattail livers that are presented here for the first time, indicate not only that PCBs, DDE, Toxaphene, and possibly Halowax (polychloronaphthalene) are present, but that the PCBs have been metabolized in a way resembling that occurring in coastal organisms, marine mammals and birds.
12. There is little evidence for food web magnification in the concentrations of PCBs, DDT and petroleum hydrocarbons in pelagic open-ocean communities, with the possible exceptions of large predatory fish such as tuna, mammals, and birds.

13. The data presented here on monooxygenase systems in deep-sea fish from two sites in the Western North Atlantic constitute a basis for comparison with any future studies of xenobiotic metabolism in deep-sea fauna. The results provide a relative measure of the capacity of deep benthic fish to metabolize foreign organic compounds, and provide direct information on the question of whether species in some deep-sea communities are presently suffering effects of exposure to biochemically significant levels of certain classes of organic compounds. The focus in this research was on fish, but the results suggest it should be possible to estimate the nature of effects in some invertebrates. Biochemical surveys in particular areas of the world's deep ocean could reveal effects there, and could suggest where surveys of fish for pathologies, including gonad dysfunction, might be warranted.

RECOMMENDATIONS

1. The question of relative susceptibility of deep-sea and shelf species cannot be answered without direct experimentation on responses to disturbance and rates of recovery.
2. The ambiguity in the modeling results demands experimental study of disturbance in the deep sea, guided by models such as those presented here. Such experiments should manipulate both the spatial and temporal scales of disturbance, should examine both population and community responses, and should consider a variety of types of disturbance.
3. Our present view of the most long-lived deep-sea species depends on the study of a single bivalve species Tindaria callistiformis. Additional radioisotopic studies of age of animals with shells should be done.
4. We must begin to obtain adequate quantitative descriptions of deep-sea communities. When this is done it will be possible to follow changes that occur in response to natural disturbance. This will require substantial support for taxonomic descriptions and systemtic studies on this poorly-known fauna.
5. There is a need for a larger data set for body burdens of organic chemical contaminants in a wider range of species with different feeding strategies and life histories. This work should be carried out in conjunction with studies on biotransformation systems and analysis of biliary metabolites.
6. In order to provide reasonable predictive models of exposure levels for deep-ocean communities, there is a need to better understand the entire biogeochemical cycle in the water column and surface sediments. The specific areas ripe for significant advancement are:
   i) dissoved, particulate matter (large and small) concentrations;
   ii) surface sediment box cores, including solid phase and solution interactions (interstitial waters);
   iii) studies of meso- and bathypelagic biology.
7. In both shallow-water and deep-water communities there is a need to better understand the relationships between chemical measurements in water, sediment and particulate matter, and bioavailability.

8. Further study of biotransformation enzymes in shelf and deep-sea animals should include: the effect of hydrostatic pressure on the function of biotransformation enzymes, relationships between steroid metabolism and xenobiotic metabolism, and potential for metabolism of specific compounds, e.g., specific PCB isomers, that are prominent contaminants.
9. The extent of apparent induction of biotransformation enzymes in the deep sea could be assessed in Coryphaenoides armatus, sampled from stations over a wider geographic area.

SECTION I: ANALYSIS OF EXISTING INFORMATION ON SUSCEPTIBILITY OF DEEP-SEA ANIMALS

J. Frederick Grassle and Judith P. Grassle

Deep-Sea Environment

Until the last two decades most deep-sea studies have emphasized the constancy of the physical environment. Sediments, chemical milieu, temperature and currents vary within extremely narrow ranges and the environment was thought to be relatively constant (Sanders et al., 1965). Although the deep sea is by no means a constant environment, the generalization is still true when the deep sea is compared to the continental shelf, where there are sharp seasonal and year-to-year differences in temperature, storm resuspension, and productivity.

The deep sea occupies five times the surface area of the continental shelves and is relatively poorly known. The main source of food for deep-sea animals derives from surface primary productivity, but only about 1% reaches the deep-sea floor (Honjo et al., 1982). Large areas of the sea floor appear to be physically quiescent, although places where the environment is more changeable have generated great interest in recent years. Off California some of the deep basins (1200-1300 m) are periodically low in oxygen (mean = 0.4 ml/l) (Jumars, 1965; Smith and Hinga, 1983). At the HEBBLE site currents have exceeded 40 cm/sec for brief periods (Hollister and McCave, 1984). In regions of intense upwelling, such as Walvis Bay, one or two species dominate the deep-sea benthic fauna (Sanders, 1969). In the Norwegian Sea filter feeders are far more common than elsewhere in the deep sea (Dahl, 1979; Dahl et al., 1976; Just, 1980). This may relate to the close coupling between bottom conditions and the sinking of productive cold surface waters. Canyons have a different epifauna compared to the depths on surrounding slopes (Hecker et al., 1980), but the differences in infauna in canyon soft bottoms have not been studied. Deep-sea trenches are known to have a benthic fauna with a comparatively low number of species, probably as a result of mud slumps (Jumars and Hessler, 1976).

Even the more stable parts of the deep sea are not unvarying. Broad expanses of the sea floor in the Western Pacific have currents that may exceed 10 cm/sec (Imawaki and Takano, 1982). An area selected for low current activity (less than 5 cm/sec) (Honjo et al., 1982) in the Panama Basin at 4000 m has frequent resuspension of the light, fluffy, surface sediments (Aller and DeMaster, 1984). The most striking variation in species distributions in these relatively stable areas results from the effects of biotic structures in and on the sediments. Glass sponges and sea pens affect the patterns of sedimentation at the surface and large unoccupied burrows may trap sediments (Grassle and Whitlatch, unpubl.; Jumars, pers. comm., Yingst, pers. comm.).

The most important environmental variation for animals relates to food settling from the surface in the form of wood, Sargassum, kelp, remains of animals, faeces and other organic aggregates. The flux of particles to the sea floor has been shown to be seasonal in the Panama Basin (Deuser and Ross, 1980; Honjo, 1982), the Sargasso Sea (Ittekkot et al., 1984), and West European Basin (Billett et al., 1983). The dispersion of sinking particles discharged in surface waters cannot be predicted with existing models, since the influence of aperiodic eddies and deep-sea storms may be opposite to the effect of net flows. This is particularly true of regions such as the Western North American Basin above 30°N where the abyssal eddy kinetic energies are high (Schmitz, 1984). Large pieces of plant or animal material that fall from the surface and the activities of large animals disrupt the normal bottom community and may prevent the development of equilibrium conditions.

Fauna:

The fauna may be considered in four separate divisions based on individual size and the methods needed for study. The microfauna includes bacteria, fungi, and soft-bodied protozoa. The meiofauna are best defined by taxonomic group: nematodes, harpacticoid copepods, foraminifera, and podocopid ostracods are the most abundant groups. Meiofaunal samples are generally less than 10 cm^2; 0.40 um screens are used to retain nematodes and 0.63 um screens to retain harpacticoids.

These two screen sizes are most frequently used in meiofaunal studies. The upper size limit is best defined by taxon especially since the occasional nematode or harpacticoid is retained by macrofaunal sieves, perhaps in a tube or incompletely washed mud ball, or tangled with bits of detritus or parts of animals. An upper size is sometimes needed for the juveniles of macrofaunal species included in the meiofauna category as temporary meiofauna. The lower sieve size for macrofaunal sampling is usually used as the upper limit for temporary meiofauna.

Since nearly all of the individuals in the dominant macrofaunal groups, such as polychaetes, bivalves, and peracarid crustacea, pass through a 1 mm sieve and most pass through a 500 um sieve, 300 um or 250 um sieves are used to set the lower size boundary in most recent studies of deep-sea macrofaunal taxa. The large animals visible on the sediment surface are defined as megafauna (Grassle et al., 1965). The literature can sometimes be confusing since, for example, Russian workers define meiofauna as the animals retained by 0.5 mm sieves, and macrofauna as the animals retained by 5 mm sieves. The extensive Russian deep-sea studies using grabs and 5 mm sieves describe neither the macrofauna nor the megafauna well. These data have mainly been used to describe broad scale differences in biomass.

The development of fine mesh trawls with closing doors (Hessler and Sanders, 1967) and large quantitative coring devices (Hessler and Jumars, 1974) has resulted in a revolution in our descriptive understanding of deep-sea communities. The most complete taxonomic work is based on trawls from the Gay Head-Bermuda transect in the North America Basin. Samples have been taken from nine other Atlantic Ocean basins, but the taxonomic work on major groups of fauna has not been completed (especially amphipods, tanaids, and polychaetes). Quantitative studies have focused on the Gay Head-Bermuda Transect, Mid-Pacific Gyre, Bay of Biscay in the Eastern Atlantic, and the deep basins off California. The number of completely processed quantitative samples (sieve size less than 0.5 mm and separation of the fauna to species) number less than 100 world-wide. Polychaetes constitute the greatest numbers of species (and individuals) in benthic samples from both the continental shelf and the

deep sea. Monographs by Hartman (1965) and Hartman and Fauchald (1967) on Gay Head-Bermuda Transect samples make this one of the more intensively studied groups in the deep sea. Despite this, box core samples occupying a total surface area of less than 5 m^2 (distributed over a range of depths from 600 m to 3000 m) contain hundreds of new polychaete species (Blake, Maciolek-Blake and Grassle, unpublished).

Diversity

By any measure the diversity of species in the deep-sea benthos is high compared with the continental shelves (Sanders, 1968; Abele and Walters, 1979; Jumas and Gallagher, 1982; Rex, 1983). Even within continental shelf environments diversity increases with depth (Maciolek-Blake et al., 1985). Predictions about local extinction of populations and community resilience have been made on the basis of species diversity alone, but the basis for such predictions is questionable (Goodman, 1975). Long-term data sets are not available from either the continental shelves or the deep sea. Buchanan (1978) describes the long-term changes in shallow (80 m) North Sea benthic fauna and long-term studies have been conducted in various shallow embayments (Bay of Concarneau - 17 and 28 m - Princz et al. 1983; Puget Sound - Lie and Evans, 1973). In the Western English Channel at depths up to 100 m there have been variations over the last 90 years in the degree of penetration of stenothermal cold-water species from the Celtic Sea (Holme, 1983). The galatheid crab Munida bamffica was rare in the 1890's, common in the 1930's and rare since 1945. The sea urchin, Echinus acutus, and a scaphopod mollusc were common in the early part of the century, but are now rare. Return of the starfish, Luidia sarsia, has been related to a climatic cycle involving changes of species in the water column. Dense beds of the brittle star Ophiothrix fragilis have fluctuated widely and were last abundant in the 1950's and 1960's. An unpublished report on Georges Bank benthos indicates remarkably stable populations of benthos at depths ranging from 60m to 170m despite seasonal effects of winter storms (Maciolek-Blake et al., 1985).

The deep-sea fauna at a permanent benthic station at 3600 m depth established in 1975 off New England has undergone a decline in density of

the entire fauna between 1978 and 1980 (Grassle, unpublished). Samples from this station in 1983 still had low densities. With very few samples from a single location it is not possible to attach a statistical significance to the changes in abundance of individual species. A widespread change in deep-sea fauna could occur without its being detected (see Jumars, 1981).

Studies at a deep-water dump site (DWD 106) used Smith-McIntyre grab samples and 0.5 mm sieves to assess changes in fauna between 1974 and 1976 (Pearce et al., 1977; Pearce et al., 1979). These methods have proven useful on the continental shelf, but do not provide the resolution needed to study the deep sea (J. P. Grassle, 1983). Densities changed from 19-49 individuals per 0.1 m^2 in 1974 to 0-14 individuals per 0.1 m^2 in 1976. The authors argue that for unspecified methodological reasons this reduction is not real. These results underscore the need for widespread acceptance of the best methods of sampling and processing the deep-sea fauna.

Rates of Population Turnover and Susceptibility of Populations

As discussed in the next section, the ability of populations to increase is closely coupled to their ability to withstand man-made or natural disturbance. Highly variable environments, such as rocky intertidal areas or mud flats, may show persistent populations despite frequent catastrophic decimation (Mettam, 1983). Information on rates of life history processes is almost completely absent for deep-sea species and life table information is lacking for both shelf and deep-sea environments. There are some data on three parameters that relate to the ability to increase -- clutch size, time to maturity, and adult survival.

Fecundity and Clutch Size

Bivalves: Most deep-sea bivalves produce hundreds of eggs. However, some of the protobranchs (e.g., Microgloma) produce one or two eggs per brood (Sanders and Allen, 1973). The main exception is the wood-boring bivalve, Xylophaga sp. that produces 35,000 eggs at each spawning (Turner, 1973). The wood habitat of this species is known to be

more ephemeral than the habitats of most deep-sea species and the high egg number in Xylophaga sp. could be related to its opportunistic mode of existence. The best within genus comparison comes from the very common bivalves of the genus Nucula (Scheltema, 1972; Allen, 1983).

	Depth distribution	Shell length (mm)	Gonad vol. (mm^3)	Gonad vol/shell length	Egg No. Per Brood	Eggs/ shell length
Nucula proxima	shelf	6.6	2.1	0.3	4120	624
Nucula annulata	shelf	3.3	0.8	0.2	1233	374
Nucula granulosa	slope	2.2	0.1	0.05	217	97
Nucula cancellata	slope	3.3	0.2	0.07	194	59
Nucula verrilli	abyss	4.3	0.2	0.06	260	60

This clearly shows that egg number and reproductive effort (the proportion of an animals's energy budget devoted to reproduction) are lower in the deeper dwelling species.

Gastropods: Rex (1979) compared populations of Alvania pelagica on the shelf with those on the slope at 800 m. The slope populations devote more energy to growth and less to reproduction. Rex (1979) notes that another gastropod, Benthonella tenella does not have a high enough fecundity to withstand heavy predation on juvenile stages. This suggests that the low number of juveniles in samples of this species are the result of its life history rather than juvenile mortality.

Echinoderms: Eggs per individual or clutch size in deep-sea ophiuroids is known in five species (Hendler, 1975):

Amphiophiura bullata	300
Amphilepis ingolfiana	500
Homalophiura tesselata	2,000
Ophiomusium lymani	200-1400 (Gage, 1982)
Ophiura ljungmani	100,000

The numbers for the first four species are low compared to shallow-water species that also have abbreviated development (viviparous species produce relatively few eggs per brood).

Pourtalesiid sea urchins (Pourtalesia jeffreysii, P. miranda and Echinosigra phiale) have 1,000 to 4,000 oocytes per individual. Deep-sea echinothuriid and cidarid sea urchins are said to have "low fecundity" compared with their shelf counterparts, but egg counts are not given (Tyler and Gage, 1984).

Ophiura ljungmani is thought to have planktotrophic development and its egg number is low compared with its shallow-water counterparts that also have planktotrophic development (250,000 to 1,000,000). It is probably an opportunistic species in the deep sea. Of the 30,000 brittle stars collected from epibenthic sled trawls from the Gay Head-Bermuda transect over 10,000 were Ophiura ljungmani from a single haul suggesting that recruitment of this species is sporadic in relation to an ephemeral favorable habitat.

Peracarid Crustacea: Two deep-sea cumaceans (Leucon jonesi and Leucon medius) studied by Bishop (1982) had 6-12 young per brood compared with 30-60 eggs per brood in a shallow-water congener (Leucon nasica). The young do not develop synchronously and may be released one or two at a time. The number of eggs per brood in the deep-sea species is lower than for any of the 17 species known from shelf waters (Carey, 1981). Deep-sea isopods produce 2-80 and most commonly 5-25 eggs per brood (Wolff, 1962). A shallow-water species from beaches, Eurydice pulchra has 33-40 eggs per brood (Jones, 1970).

Fish: Egg numbers of fish may be as high as 10,000 to 20,000 and no clear generalization is apparent relative to the life histories of deep-sea and shelf fish (Marshall, 1979).

Time to Maturity

Turekian et al. (1975) estimate a time to maturity of the bivalve, Tindaria callistiformis, of fifty years. Since this estimate is based on

only four size classes, it may be in error by as much as 50%. In colonization trays Grassle (1977, 1980) found one species of bivalve that reached maturity in two years (Nucula cancellata) and a tunicate (Polycarpa delta) that reached maturity in about one year. A species in the opportunistic polychaete genus Capitella reached maturity in about one year, assuming settlement shortly after placement of the experimental tray. Most shallow-water species of Capitella take about one month to mature, but maturation may be longer in some of the annual species with planktotrophic larvae. The deep-sea wood borer, Xylophaga sp., takes only three months, but, like Capitella, we expect this species to be well-adapted to its ephemeral, food-rich environment by rapid maturation and a potential high rate of population increase.

Colonization

Rates of colonization of trays of azoic sediment indicate lower rates of colonization of most species in the deep sea (Grassle, 1977, 1980). The number of individuals are an order of magnitude lower than in surrounding sediments after two years and most individuals are juveniles. Some species in the deep-sea such as Capitella spp., spionids and Ophryotrocha spp. colonize rapidly if the sediments are rich in organics (Desbruyerēs et al., 1980; Hecker, 1982). Boesch and Rosenberg (1981) have reviewed the data on colonization rates, and indicate faster rates on the continental shelf at 65 m depth (after 9 months the trays had one-half the species and one-quarter the individuals in comparison to the natural community). Similar results have been found by Virnstein (pers. comm.) for experiments at 33 m and 187 m depth off Fort Pierce Inlet, Florida: within 6 weeks densities were three times control densities at the shallow site and densities at 187 m were an order of magnitude lower and still increasing at the end of 12 weeks.

Adult Survival

Literature reviews of the average life span for shallow water invertebrates (Robertson, 1979; Wildish and Peer, 1983) indicate most species found on the continental shelf live from one to three years.

A detailed study of life history and productivity of three species of amphipods over a three year period on Georges Bank found maximum life spans of 6 to 8 months, 18 months, and two years for Erichthonius rubricornis, Unciola inermis, and Ampelisca agassizi respectively (Collie and Curran, 1985). The polychaete Aricidea catherinae on Georges Bank appears to have a two year life cycle (Blake and Baptiste, 1985). These estimates are for those few species that produce a clear enough pulse of offspring to be seen as a cohort in sequential sampling. Buchanan found at least two species, the bivalve, Thyasira sp. (Buchanan and Warwick, 1974) and a burrowing shrimp, Calocaris macandreae (Buchanan, 1963) that have life spans of 8 and 15 years. The longest-lived polychaete in Buchanan's study was Glycera rouxi with a five year life span. Another polychaete, Scoloplos sp. , in subarctic regions also lives this long (Hardy, 1977). A few megafaunal bivalves, echinoderms, decapods, and anemones, may live 20 years (Wildish and Peer, 1983), and Arctica islandica is known to live at least 90 years (Thompson et al., 1980; Turekian et al., 1982).

Estimates of longevity in the deep sea are few. The largest size class of the bivalve, Tindaria callistiformis, was estimated to be 100 years old using ^{228}Ra dating techniques (Turekian et al., 1975). Adult individuals of T. callistiformis have 100 growth rings in the shell. This provides independent support for the radiotracer estimate only if the rings are a result of an annual pulse of productivity reaching the bottom. Hutchings and Haedrich (1984) studied shelf bivalve species, Nuculana pernula and Yoldia thraciaeformis, whose populations extend to bathyal depths (900-1500 m). These species reach a much larger size than most deep-sea bivalves with maximum recorded lengths of 3 cm and 5.5 cm. If growth bands can be used to estimate age, the oldest individuals of these species are 10 years and 13-15 years. Such ages are not unusual for large shelf bivalves. Ages of soft-bodied deep-sea animals are completely unknown.

Ages of fish have been estimated from otoliths and in one instance this has been confirmed by $^{210}Pb/^{226}Ra$ measurements. Sebastes diplora from the outer continental shelf and upper continental slope has a longevity of about 80 years (Bennett et al., 1982).

Timing of Reproduction

A number of studies indicate that some deep-sea echinoderms and molluscs reproduce seasonally (reviewed by Tyler et al., 1983). Most of these studies were of animals from regions where there is a dense spring bloom of algae (e.g., brittle stars on the Gay Head-Bermuda transect and bivalves and echinoderms from the Rockall Trough off Scotland). Recent sediment trap studies (Deuser and Ross, 1980; Honjo, 1982) and time lapse photographs confirm the seasonal pulse of surface productivity reaching the bottom (Billett et al., 1983). The only animals in the San Diego Trough showing seasonal reproduction were a scaphopod and brachiopod whose distributions extended up onto the continental shelf (Rokop, 1977). Sea anemones from 2000-2500 m in the Bay of Biscay off the coast of France showed evidence of spring spawning (Van Praet and Duchateau, 1984).

Dispersal and Biogeography

Most deep-sea species have comparatively large yolky eggs that are usually thought to indicate limited dispersal ability. The discovery of hydrothermal vent species with yolky eggs that are able to colonnize relatively ephemeral vent sites separated by at least hundreds of kilometers calls this generalization into question. The most diverse group of deep-sea species, the peracarids (amphipods, isopods, tanaids, cumaceans), brood their young and are presumed to have the most limited powers of dispersal. These groups have the most limited depth distributions and greatest endemicity (for example, 40% of cumacean species are endemic to the North American Basin (Jones and Sanders, 1972)). The larvae of deep-sea gastropods spend their early stages of development in surface waters before migrating back to the deep sea (Rex and Waren, 1981; Killingley and Rex, 1985). This sort of dispersal may occur in some groups of polychaetes, but there is no definite evidence (Bhaud, 1983).

The eggs of many deep-sea fish float to the surface and the larvae are transported in surface currents (Marshall, 1979). Although the larvae of rattails (Macrouridae) are rare, the youngest stages are found above the thermocline (Stein, 1980).

Feeding

In the deep sea, suspension feeders are relatively rare and most species feed on particles on or just below the sediment surface (Jumars and Gallagher, 1982). Carnivores may make up 2-13% of the fauna, but this mode of feeding usually cannot be distinguished from that of scavengers or omnivores (Jumars and Gallagher, 1982). For example, brittle stars are mostly omnivores (Pearson and Gage, 1984). Well-known abyssal scavengers include the amphipod, Eurythenes gryllus (Ingram and Hessler, 1983) and rattail fish (Macrouridae) of the genus Coryphaenoides (Macpherson, 1981; Mauchline and Gordon, 1984; Pearcy and Ambler, 1974; Sedberry and Musick, 1978). Large sea urchins, brittle stars and quill worms may also be attracted to concentrations of organic material (Grassle et al., 1965; C. Smith, in press). The distance traveled by these scavengers is not known.

The deep-sea gastropod fauna includes a greater proportion of predators at intermediate depths (Rex, 1976). Of the order Mesogastropoda 32% of the species are predators in shallow water (Tsikhan-Lukanina, 1982) whereas less than 4% are predators in the deep sea (Rex, 1976). The proportion of individuals collected that are predators is best understood in terms of individual species. The deposit feeding mesogastropod Benthonella tenella makes up two thirds of the gastropod fauna at depths below 3800 m and another mesogastropod Alvania forms about one-quarter of the fauna at depths less than 1200 m (Rex, 1973). The increased proportion of predators at intermediate depths is due mainly to the neogastropod, Manzilia bandella.

Physiology and Biochemistry

Rates of metabolism of deep-sea animals are generally low. This is true of bacteria living free in deep-sea sediments (Jannasch and Taylor, 1984), benthopelagic animals and possibly the relatively sessile animals living in or on sediments (Smith and White, 1982). Bacteria with optimum growth at high pressure have been obtained only from the guts of deep-sea invertebrates (Yayanos and Dietz, 1979; Deming and Colwell, 1982; Jannasch and Taylor, 1984). Oxygen uptake of whole sediments studied in situ correlates with depth and primary productivity of surface waters in the Pacific (ml O_2/m^2 hr respiration = 0.3508-0.000142 m depth + .007680 gC/m^2 yr primary productivity). The equation is based on 7 stations and accounts for 99% of the variance in respiration (Smith and Hinga, 1983). The equation: ml O_2/m^2 hr respiration - 0.0200 m depth + 0.0043 individuals/m^2 macrofaunal abundance also explains 99% of the variation in respiration (Smith and Hinga, 1983). The latter suggests that the low sediment respiration rates are, in part, a result of lowered macrofaunal respiration rates. The bottom dwelling (benthopelagic) fish Coryphaenoides armatus and Coryphaenoides acrolepis have very low rates of metabolism and these rates are significantly lower than for the phylogenetically related Atlantic cod (Gadus morhua) (Smith and White, 1982). Midwater fish show metabolic rates correlated with minimal depth of occurrence with fish living entirely below 200 m having uniformly low rates of oxygen consumption (Somero, Siebenaller and Hochachka, 1983; Childress and Somero, 1979). Rates of oxygen uptake for these species are correlated with activities of muscle enzymes, lactate dehydrogenase, malate dehydrogenase, pyruvate kinase and isocitrate dehydrogenase ($r = 0.82, 0.92, 0.91$ and 0.69) (Childress and Somero, 1979). If this relationships holds for bottom dwelling fish then three other species of Coryphaenoides (C. rupestris, C. capinus and C. leptolepis) and Nezumia bairdii will have a low rate of oxygen consumption like Coryphaenoides armatus. The low metabolic rate of deep-sea fish is attributed to their feeding habits and locomotory habits (Somero, Siebeneller and Hochachka, 1983). The deep-sea fish may adopt more of a "sit-and-wait" or "float-and-wait" predatory strategy. They may also not need as rapid

escape responses to avoid larger predators as their shallow-water relatives. Deep-sea benthopelagic megafaunal species tend to be neutrally buoyant, hovering motionless with little expenditure of energy (Marshall, 1979).

The tolerance of deep-sea animals to anthropogenic materials and other forms of environmental change such as smothering by sediment is unknown. Less intense resuspension and transport of sediments and relative constancy of the chemical regime suggest that few species will be pre-adapted to either new chemicals or heavy sedimentation of materials from the surface (or in situ mining activities). Shelf species on the other hand withstand heavy erosion and redeposition of sediments and are exposed to a wider range of chemicals discharged from rivers and runoff from land. Despite theoretical predictions, direct in situ experimentation with various environmental perturbations in the deep sea is of utmost priority. In addition to the more easily collected scavengers, studies of toxicity should include species that live exclusively in deep-sea sediments.

Biochemistry

Modes of protein synthesis, molecular polymerization and enzyme structure have evolved to allow deep-sea species to function at rates determined by ecological relationships of deep-sea species. Enzymatic reactions require changes in the organization of water around metabolic intermediates and protein amino acid side chains are likely to result in an increase in system volume during reactions. Single amino acid substitutions have been shown to allow enzymes to operate independently of pressure with the loss of some catalytic efficiency (Somero, Siebenaller and Hochachka, 1983). Activation of polymerization of actin in deep-sea fish has been shown to require greatly reduced changes in system entropy (Hochachka and Somero, 1984) compared with entropy change associated with actin polymerization in shallow-water species.

Genetic Variation

Species of deep-sea megabenthic invertebrates show a greater degree of genetic variation in the deep sea than their shallow-water relatives (Ayala et al., 1975; Ayala and Valentine, 1974; Murphy et al., 1976; Gooch and Schopf, 1972). These species are widely dispersed as larvae, and each local biotic environment is likely to select for different genetic alternatives (alleles) at each locus (Grassle and Grassle, 1978). High genetic variation also seems to be characteristic of tropical species with life histories not unlike the deep-sea species that have been studied. Studies have not been done on those macrofaunal invertebrates with limited ability to disperse their offspring widely. If these species with limited dispersal ability have low genetic variability then these species would be the most susceptible to extinction in the form of a widespread change in the environment.

Hydrothermal Vents

The animal communities at hydrothermal vents provide a contrast to deep-sea communities elsewhere. Adaptations to an ephemeral yet concentrated source of food by an entire community of animals, in many cases different from other known species at the family level, confirm the notion that rates of biological activity in the deep-sea have evolved in response to the pattern and timing of energy input. The main source of food for hydrothermal vent animals is the chemosynthetic vent bacteria that use CO_2 as a carbon source and derive energy from sulfide and other reduced compounds in the hydrothermal fluid emanating from vents. The large Riftia pachyptila (worms), Bathymodiolus sp. (mussels), and Calyptogena magnifica (clams) that characterize the Galapagos vents all have symbiotic bacteria that provide a significant portion of the energy needs of these animals. Many of the other vent species filter particles from the waters that contain chemosynthetic bacteria. The biomass of Riftia and Bathymodiolus at the Galapagos Rose Garden vent may exceed 20 kg/m^2 (Hessler and Smithey, 1983).

The presence of a number of vents with only dead shells that dissolve in less than 15 years (Killingley et al., 1980; Lutz et al., 1983) indicate that vent fields frequently die out after one or two decades. Theoretical calculations on rates of heat loss and solidification of subsurface rock at 350° vents also suggest that active vents persist for about ten years (MacDonald et al., 1980). Mussels and clams reach maturity in 3 years (Berg, in press), even at deep-sea temperatures, if they are in a source of hydrothermal fluid. Maximum age is 14 years for the mussels (Rhoads et al., 1982) and about 20 years for the clam (Lutz et al., 1983; Turekian et al., 1983). The mussel has planktotrophic eggs and the remaining vent species (including 7 new families of limpets) have lecithotrophic eggs (Lutz et al., 1979). Egg numbers have not been calculated but they are in the thousands.

Rates of respiration of mussels and crabs are similar to those of relatives living at shelf depths (Mickel and Childress, 1982; Smith, in press). Rates of microbial turnover are extremely high when determined using similar experimental techniques to those used in other places in the deep sea (Jannasch and Taylor, 1984).

Studies of vents confirm that metabolic rates are not limited by the high pressures in the deep sea. Since most of the vent animals live away from elevated temperatures this too is not an important factor. Food supply is clearly important, but the fact that populations rapidly exploit food to maximize production of large numbers of offspring to colonize new vents may be even more important. In other words, the vent species, like the deep-sea species adapted to exploit rare pieces of wood, respond to an ephemeral local environment and have opportunistic life histories.

CONCLUSIONS

None of the parameters needed to predict relative sensitivity of continental shelf and deep-sea communities are esimated for the whole range of species in the deep sea and there is overlap in the range of life history features in the two environments. The least ambiguous life history comparison can be made for maturation time. The majority of species in shelf sediments reach maturity in a year or less. From mud tray experiments, only a very few species reach maturity in a year or less in the deep sea.

Fecundity of deep-sea animals has not been measured directly, however, a lower rate of fecundity in deep-sea species can be inferred from lower egg numbers per individual (clutch size). In mud trays colonization rates and population growth rates are much lower in the deep sea then in shallow water. Precise estimates are not possible but on the average the difference is likely to be more than a factor of two. Intrinsic rate of increase is even more difficult to estimate but the difference is in the same direction and may be of similar magnitude.

Carrying capacity is lower in the deep sea because of the low rates of food supply from surface waters. There is a broader range of species densities on the continental shelf. This suggests a greater coefficient of variation in carrying capacity or population growth rate in shallow-water populations.

The spacing of newly settled colonists in mud trays indicates less intense competition among juvenile stages in the deep sea. These experimental conditions may occur rarely so that it is not possible to compare intensity of competition in the two environments. The lower proportion of juveniles in deep-sea populations may be a reflection of lower fecundity or relatively higher juvenile than adult mortality.

Relative to shallow water, disturbance in the deep sea is mostly biogenic and of much smaller spatial scale. This means that for any given site on the sea floor disturbance is less frequent.

Rates of population processes in hydrothermal vent communities lead to opposite conclusions in comparison to deep-sea populations elsewhere

(more rapid maturation time, higher fecundity and population growth rate, and greater proportion of juveniles). This is attributed to the greater disturbance frequency resulting from the ephemeral natural of the hydrothermal vent environment. Hydrothermal vent species also have unusual abilities to disperse and colonize new environments. The clear contrast between hydrothermal vent populations and other deep-sea populations supports the contention that the rates are determined, at least in part, by the patterns of disturbance and food supply. Even though the amount of information is meager in both instances, the differences between these two deep-sea environments are obvious.

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For Literature Cited, please see APPENDIX I.

APPENDIX I

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Section II: Identification of Population and Community Parameters Determining Relative Sensitivity

Hal Caswell

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II.1 Introduction

II.1.1 Goals

This section presents the results of our attempts to identify the life history characteristics and community parameters which determine the relative sensitivity of a community to disturbance, especially the sorts of disturbance associated with anthropogenic inputs. We will study models of disturbed populations and communities, and study the factors determining their sensitivity to disturbance. By comparing these factors with the properties of deep sea and continental shelf systems summarized in the preceeding section, we can draw conclusions about the relative sensitivity of the two systems.

We report here on three quite different models: (1) a single species population model, (2) a spatially homogeneous community model focusing on interspecific competition, and (3) a spatially heterogeneous community model including dispersal and local extinction.

It should be recognized at the outset that this attempt raises exceedingly difficult theoretical questions. One is reminded of the debate over the relation between diversity and stability. Had this debate been resolved unambiguously its results might solve the present problem, since one of the distinguishing features of the deep sea is its generally high diversity. Unfortunately, it produced no clear-cut answers.

Initially, the answer seemed intuitively obvious. Elton (1958) claimed that diverse communities were more resistant to perturbation because

> "Mathematical concepts about the properties of the food-chain, and simplified laboratory experiments, prepare our minds for instability in very simple population systems.... Oceanic islands and crop monocultures are simple ecosystems that show high vulnerability to invasions...and frequent outbreaks of population subsequently. But tropical rain forest has these features damped down to a remarkable degree." (p.150)

MacArthur (1955) similarly argued that stability should increase as the number of food chain links in the community increases, as the number of species increases, and as the dietary diversity of the species increases.

Watt (1965), on the other hand, argured that high diversity in one trophic level actually reduces the stability of lower trophic levels because increased competition prevents the species in the higher trophic level from responding to, and thus regulating, fluctuations in the lower trophic level. By the mid 1970's more detailed theoretical analyses (May 1975, Goodman 1975, Caswell 1976) and empirical surveys (Connell 1978) all concluded that there is no consistent causal relation between diversity and

stability, certainly none strong enough that its conclusions should be used to manage an ocean dumping program.

To an extent, this controversy rested on a continual uncertainty about the meaning and measurement of "stability". Well defined mathematical meanings (e.g. local stability, in the sense of Lyapunov, of an equilibrium point of a system of differential equations) did not, in general, capture the properties of communities which the biologists were talking about. The exact meaning of "diversity" was equally vague.

In the context of the present report, we note that there is no single consistent definition of what it means to say that a system (population or community) is more or less sensitive. Sensitivity might be measured by changes in growth rates, abundances, species composition, species diversity, trophic patterns or the relative abundance of functional groupings of species. A system might be classified as less sensitive if it is resistant to a given perturbation, or if it is less resistant but returns more rapidly to its original state. One's stand on such issues is likely to reflect one's opinion on such ecological questions as the equilibrium status of communities (see below) which are unresolved in general, let alone in the deep sea.

To make matters worse, the perturbations with reference to which sensitivity is, by definition, measured are also various. Disturbance in the deep sea can be expected to kill some organisms outright, to change the survival, growth and reproductive rates of others, and to do so in spatially and temporally heterogeneous ways. Thus generalities about the relative sensitivities of the two environments will involve very significant amounts of ecological theory.

Our models will examine several different measures of sensitivity:

(1) changes in population growth rate (and by extension population size) in response to perturbations in demographic parameters,

(2) changes in local species richness in response to perturbations which kill individual organisms in a non-selective fashion, and

(3) changes in regional abundance and species richness in response to perturbations which destroy local patches of habitat.

Other possibilities could, of course, be studied.

II.1.2 Models

II.1.2.1 On Generality, Realism and Precision

Models may be classified according to their generality, their realism and their precision (Levins 1966). It is a fundemental methodological principle that no model can simultaneously maximize all three of these characteristics. Any model must choose to

sacrifice at least one of the three in an attempt to maximize one or two of the others. Given this restriction, it is important to understand where our models fall, and why we made the choices we did.

Generality refers to the range of applicability of a model. General models can be applied to a wide range of situations (e.g. habitats); specific models are tailored to the description of individual situations. The task set for this project demands models with a high degree of generality, because NOAA is seeking advice not on the response of any specific location in the deep sea but on the likely responses of deep sea communities in general, compared to those of continental shelf communities in equal generality.

The realism of a model is determined by the extent to which it attempts to include important biological factors and processes in realistic fashion. Because we must make predictions about the results of perturbations, we must include those processes which are likely to determine the response to those perturbations, and hence have attempted to construct reasonably realistic models, within the limitations of the available information on the differences between deep sea and shelf populations and communities.

Precision refers to the ability of a model to make quantitative, numerical predictions of system behavior. Because we have been compelled to strive for generality and realism, we have chosen to sacrifice precision almost completely. As is appropriate given the nature of the questions posed by NOAA, and the data on the general differences between the deep sea and the shelf, our conclusions are qualitative rather than quantitative. Given this fact, it is inappropriate to ask whether "hard data" are available to provide numerical estimates of the parameters in these models. The relevant question is whether the qualitative differences in community response predicted by our models do in fact correspond to the qualitative trends in the parameters which are supposed to generate them.

II.1.2.2 Some General Assumptions

Our community models view both deep sea and continental shelf communities as nonequilibrium assemblages. That is, we do not suppose that the species co-occurring at a given spot represent the stable equilibrium of some set of interspecific interactions (typically competition). Instead, we assume that some of those species are unable to persist permanently, and are destined for local extinction. On a regional scale, such local extinction is balanced by dispersal into open patches of habitat created by biotic or abiotic disturbance. On a regional scale, such nonequilibrium species may be abundant and frequently found in close association with their competitors.

Such a nonequilibrium perspective focuses attention on a very different set of community properties than does the more

traditional equilibrium view. Spatial heterogeneity, the time scale of local interactions, the frequency of disturbance and the pattern of dispersal and colonization are crucial parameters for understanding nonequilibrium communities.

Our choice of the nonequilibrium perspective is based on the evidence, now accumulated for many different communities, that natural disturbance processes are an important component of the environment, that community structure reflects these processes, and that local extinction is a common process (see Sousa (1984) for the best recent review). The theoretical community ecology of the 1970's was organized around models of the equilibrium properties of spatially uniform systems. These assumptions (equilibrium and uniformity) effectively remove considerations of spatial and temporal scale from consideration. However, those very scale considerations are crucial in attempting to predict the results of added anthropogenic disturbance.

Each of our models includes disturbance, but each describes the process of disturbance in a different way. In our single species demographic model, disturbances alter the values of demographic parameters: juvenile survival, adult survival, adult reproductive rate and maturation time. In the first of our two community models, disturbances reduce the densities of all species in the community by a specified proportion, and are characterized by their frequency and intensity. In the second community model, disturbances are randomly distributed in space and, when they occur, completely decimate local patches of habitat. Disturbance is characterized by its frequency and the nature of the colonization process which follows a disturbance. The differences between these descriptions of disturbance are probably not trivial, but each of them no doubt contains some aspects of the "true" effect of disturbance due caused by waste dumping.

II.1.2.3 Biotic Impoverishment or Intermediate Disturbance ?

As will be shown in more detail in subsequent sections, one of the major predictions of nonequilibrium community theory is that diversity should be maximized at intermediate frequencies and intensities of disturbance (Connell 1978, Huston 1979, Sousa 1984). Too much disturbance eliminates species directly; too little allows them to be eliminated by competition. From this perspective, disturbance is often a positive influence, responsible for much of the diversity and structure which communities posess.

In contrast, disturbance is also often seen as leading to "biotic impoverishment": shortened food chains, decreased diversity, and dominance by a handful of species hardy enough to resist the disturbance (Woodwell 1983). Such patterns of impoverishment are well documented in terrestrial plant communities subjected to radiation stress and air pollution, in polluted aquatic habitats and in overgrazed rangeland, among other habitats.

Unifying the biotic impoverishment and the intermediate

disturbance perspectives is not easy, but at least three possibilities present themselves. The first is based on disturbance frequency. The disturbances which lead to biotic impoverishment are chronic at any one spot, while the disturbances which lead to increased diversity tend to be transient at any one spot. In a sense, biotic impoverishment is caused by a disturbance which just won't quit and allow the community to recover. Overgrazing of range land is an excellent example; Whittaker (1975) presents this as an example of biotic impoverishment effects, but grazing at intermediate intensities is well known to increase diversity (Harper 1969), and to be more spatially and temporally intermittent than grazing at inermediate intensities (Caswell 1978a). Other such examples exist. Pearson (1980), for example, found maximum benthic diversity at an intermediate distance from a toxic effluent outfall, but closer to the outfall this disturbance clearly resulted in biotic impoverishment.

A second possibility is that biotic impoverishment results from disturbances to which the biota is not adapted, so that the community comes to be dominated by those few species that can tolerate the stress. The adaptation in question may not be that of the organisms immediately affected by the disturbance, but of the rest of the population. Rocky intertidal organisms, for example, are not "adapted" to being scraped from from their homes or bashed to bits by floating logs; this disturbance undoubtedly kills almost all the individuals it affects. What the intertidal species are adapted to is to colonizing and thriving under the conditions remaining after such a disturbance has passed. This adaptation is expressed by the offspring of individuals who escaped the disturbance.

Some disturbances, especially anthropogenic ones, delay such recolonization for for a long time. Levin and Smith (1984), for example, examined the recolonization of defaunated sediment at 1300 m in the Santa Catalina basin. They found that defaunated sediment was recolonized slowly (as is usually the case in the deep sea), but that defaunated sediment enriched by kelp was essentially uncolonized by macrofauna during the course of their study. Thus disturbance of this system associated with falls of kelp tissue to the bottom could be expected to have long-lasting residual effects. As we will see below, such residual effects make it less likely that the disturbance will lead to increases in diversity. It may be that such evolutionarily new disturbances as toxic wastes are more likely to have long-lasting residual effects; if so anthropogenic disturbance is more likely than natural disturbance to cause biotic impoverishment.

1.3 Acknowledgements

I would like to acknowledge the programming assistance of Daniel W. Smith, especially with the models described in II.2 and II.3. The model of section II.4 was developed in collaboration with Dr. Joel E. Cohen.

II.2. Single Species Model

II.2.1 Model Structure

This model is based on the life cycle graph shown in Figure 1. This life cycle is defined by four parameters: age at maturity (α), the probability of survival from birth to maturity (P_1), adult survival probability (P_2) and per-capita fecundity (F). This model implicitly assumes that adult survival and fecundity are age invariant after reproductive maturity and that all individuals become mature at essentially the same age.

From these four demographic parameters, we can calculate the eventual population growth rate λ (λ is the discrete time rate; the continuous time "intrinsic rate of increase", $r=\ln(\lambda)$ is often used instead). It is the solution to the characteristic equation (see Caswell 1982b for derivation of this equation)

$$1 - P_1 F \lambda^{-\alpha} / (\lambda - P_2) = 0 \qquad (2.1)$$

This growth rate combines survival, growth and reproduction into an integrated measure of population success. It has been used in laboratory experiments to describe the effects of toxic substances (e.g. Daniels and Allan 1981, Allan and Daniels 1982), radiation stress (e.g. Marshall 1962), food supply (e.g. Hall 1964), temperature (e.g. Birch 1953), and so on. At the coarsest level, it also determines persistence, since $\lambda<1$ implies eventual extinction, while $\lambda\geq 1$ implies population growth.

Given the right assumptions, changes in the value of λ can also be related to changes in population size. In nature, the long term average value of λ for a persisting population must approach 1 (less than this would imply extinction, more than this an unreasonable exponential increase in numbers beyond any reasonable limit). If one assumes that populations are typically near a density-dependent equilibrium (a questionable assumption!) then variation around the long term mean of 1 will be small. In such cases, the effects of a perturbation on equilibrium population size will be <u>directly proportional</u> to the effects on λ. In nonequilibrium populations, of course, natural variation in population size is large enough that it is unreasonable to use it as a measure of sensitivity.

Environmental perturbations may change development rates, survival probabilities, and/or fecundities; those changes in turn affect the value of λ. The sensitivity of λ to changes in each of the life cycle parameters can be derived from (2.1) by implicit differentiation (i.e., for example, writing (2.1) as $f(\lambda, P_1)=0$,

$$\partial\lambda/\partial P_1 = -(\partial f/\partial P_1)/(\partial f/\partial\lambda)):$$

Applying this to (2.1) for each of the demographic parameters yields:

$$\partial\lambda_1/\partial P_1 = F\lambda_1^{1-\alpha}/((\alpha+1)\lambda_1-\alpha P_2) \quad (2.2a)$$

$$\partial\lambda_1/\partial P_2 = \lambda_1/((\alpha+1)-\alpha P_2) \quad (2.2b)$$

$$\partial\lambda_1/\partial F = P_1\lambda_1^{1-\alpha}/((\alpha+1)\lambda_1-\alpha P_2) \quad (2.2c)$$

$$\partial\lambda_1/\partial\alpha = -\lambda_1 \ln(\lambda_1)(\lambda_1-P_2)/((\alpha+1)-\alpha P_2) \quad (2.2d)$$

Equations (2.2a-d) give the sensitivities of λ_1 to changes in each of the parameters taken singly. Perturbations due to toxic waste dumping will, of course, change more than one demographic parameter at the same time. To evaluate the effect of such variations, we can also calculate two overall sensitivity indices (cf. Caswell 1978b):

$$S_1 = [(\partial\lambda_1/\partial P_1)^2 + (\partial\lambda_1/\partial P_2)^2 + (\partial\lambda_1/\partial F)^2 + (\partial\lambda_1/\partial\alpha)^2)]^{1/2} \quad (2.3)$$

$$S_2 = [P_1(\partial\lambda_1/\partial P_1)^2 + P_2(\partial\lambda_1/\partial P_2)^2 + F(\partial\lambda_1/\partial F)^2 + \alpha(\partial\lambda_1/\partial\alpha)^2)]^{1/2} \quad (2.4)$$

S_1 is effectively the standard deviation in λ_1 that would be generated by independent random variation, with unit variance, in each of the parameters. S_2 takes into account the fact that P_1, P_2, F and α are measured on quite different scales, and gives the corresponding standard deviation in λ_1 generated by independent variances proportional to the mean of each parameter. In neither case do we expect precisely such variation to be present in the environment; instead, S_1 and S_2 should be taken as two overall sensitivity measures which weigh the contributions from the different parameters in different ways.

Given a life cycle model and a set of sensitivity indices, our questions are (1) what parameters determine the relative values of these sensitivities, and (2) can we expect deep sea populations to differ in any consistent fashion from shelf populations in their degree of sensitivity?

II.2.2 Methods

To approach the first question, we reasoned that in nature there is wide interspecific variation in each parameter. Thus values for P_1, P_2, α and F were drawn at random from the following distributions:

P_1: log-uniformly distributed between .00001 and .01

P_2: log-uniformly distributed between .01 and 1.

F: log-uniformly distributed between 10 and 1,000,000

α: uniformly distributed between 5 and 50.

The characteristic equation (2.1) was solved for λ_1 for each of the parameter sets, and then the sensitivities were evaluated from (2.2-2.4). This produces a data base from which we can hope to

untangle the factors determining sensitivity.

Figure 2 shows the distribution of values of λ in a sample of 1000 such life histories. It is very close to lognormal, with a mean very close to λ=1 (mean = 1.0426, s.d. = .245), suggesting that our sampling ranges are biologically reasonable. (Any such sampling procedure generates results which depend on the area of parameter space sampled. In the present case, another run with the P_1 log-uniformly distributed between .01 and 1 and F log-uniformly distributed between 1 and 10^6 produced results indistinguishable from those which follow.)

To identify the factors determining each of the sensitivity indices, we used stepwise multiple regression (BMDP Procedure P2R, Dixon 1981) to fit an equation describing each index ($\partial\lambda/\partial\alpha$, $\partial\lambda/\partial P_1$, $\partial\lambda/\partial P_2$, $\partial\lambda/\partial F$, S_1 and S_2) as a function of the independent variables P_1, P_2, F, α, and λ. All the independent variables, and all the sensitivity indices save $\partial\lambda/\partial\alpha$ (which may be negative), were log transformed before analysis. Letting X denote any of the sensitivity indices except $\partial\lambda/\partial\alpha$, the regression model was

$$\log X = a + b*\log(P_1) + c*\log(P_2) + d*\log(F) + e*\log(\alpha) + f*\log(\lambda)$$

For $\partial\lambda/\partial\alpha$ the model was

$$\partial\lambda/\partial\alpha = a + b*\log(P_1) + c*\log(P_2) + d*\log(F) + e*\log(\alpha) + f*\log(\lambda)$$

The regression coefficients b-f show how the sensitivity indices depend on each of the demographic variables. In the log-log model, the coefficients give the proportional change in X resulting from proportional changes in the dependent variables. A value of b=0.5 (-0.5), for example, implies that a 10% increase in P_1 produces a 5% increase (decrease) in X.

II.2.3 Results

The regression coefficients and R^2 values are shown in Figure 3a-f. The model fitting procedure was quite successful, as evidenced by multiple R^2 values between .7014 and .9955. Figure 3a, for example, shows that $\partial\lambda/\partial P_1$ is directly proportional to λ, inversely proportional to P_1 and α, and essentially independent of the values of P_2 and F. Thus populations with high values of λ and low values of P_1 and α are expected to be particularly sensitive to perturbations which change the value of P_1.

Summarizing the results shown in Figure 3, the following conditions imply <u>higher sensitivity</u> to any given level of variability in the demographic parameters:

$\partial\lambda/\partial P_1$: low P_1, low α, high λ
$\partial\lambda/\partial P_2$: high P_2, low α
$\partial\lambda/\partial F$: low α, low F, high λ
$\partial\lambda/\partial\alpha$: high P_1, low α, high F, low λ
S_1: low P_1, low α, high λ
S_2: low P_1, low α, high λ

II.2.4 Conclusions

II.2.4.1 The Determinants of Demographic Sensitivity

Although the coefficient patterns for the different sensitivity indices differ, the overall results suggest that populations with rapid development, low survival to maturity, low fecundity and high population growth rate should be more sensitive to demographic perturbations than populations with the alternative characteristics. Adult survival probability is generally unimportant. In particular, both of the overall sensitivity indices S_1 and S_2, decrease with P_1 and α and increase with λ.

II.2.4.2 The Relative Sensitivity of Deep Sea Populations

The available data on deep sea populations (Grassle, this report) suggest that they are characterized by higher values of α and lower values of F than shelf populations. If the general rarity of juveniles in the deep sea results from high (and perhaps variable) juvenile mortality, then P_1 is also lower in deep sea populations. It is likely that the realized values of λ are lower in the deep sea, since λ itself is strongly dependent on α and F (Caswell and Hastings 1979).

Based on these differences, our results predict no consistent differences in sensitivity between deep-sea and shelf populations. In the case of only one of the sensitivity indices ($\partial\lambda/\partial P_2$) can one make an unambiguous prediction: that deep sea populations are less sensitive than shelf populations. All the other indices are ambiguous because the differences in parameters between the two habitats imply both greater and lesser sensitivity in the deep sea.

II.3. Spatially Homogeneous Communities Subject to Disturbance.

II.3.1 Background: Disturbance Effects.

Communities are disturbed by a variety of natural processes, both biotic (predation, habitat alteration due to burrow construction, bioturbation, etc.) and abiotic (e.g. landslides, storms, forest fires). It is now widely recognized that such disturbances are an integral part of community dynamics which must be taken into account in theories of community structure.

The most studied aspect of disturbance is its effect on coexistence and diversity. This impact was once thought to be uniformly negative, diversity being maintained only in spite of disturbance. From such a perspective, the only likely effect of additional, anthropogenic disturbance is a syndrome Woodwell (unpublished) terms "biotic impoverishment": reduced species and life form diversity, higher dominance, greater representation of small-bodied or low-growing forms, simplified interaction patterns and reduced production.

Disturbance, however, has positive as well as negative effects on coexistence and hence on diversity. This possibility has been recognized at least since Hutchinson (1951, 1953) introduced the terms "fugitive species" and "nonequilibrium species" to describe species which rely on disturbance to interrupt the process of competitive exclusion, either by temporarily changing conditions or by creating new patches of habitat in which they may persist until excluded by competition. It is often assumed that such species are "weedy", short-lived and ephemeral, but it has become clear within the last decade that disturbance may mediate the persistence of even large, long-lived species (Caswell 1982a) and it may well be the case that the majority of species persist only because disturbance maintains locally nonequilibrium conditions.

Suprisingly little attention has been paid to the problem of what determines whether the effect of disturbance on diversity is positive or negative. An interesting conjecture was provided by Hutchinson (1953), who proposed that the effect of disturbance depends on its time scale relative to the time scale on which competition operates. Disturbance operating on much faster or much slower time scales than competition should have little effect on the rate of competitive exclusion, but if the two time scales are commensurate disturbance should greatly delay competitive equilibrium.

This conjecture has never been rigorously examined, but it has been widely accepted as one of bases of the "intermediate disturbance frequency" hypothesis: that diversity should be maximized by an intermediate frequency of disturbance, and decreased by either too frequent or too infrequent disturbance (e.g. Connell 1978, Huston 1979). This prediction is now supported by empirical studies on a variety of disturbance

processes (e.g. Osman 1977, Sousa 1979, Lubchenco 1978, Hixon and Bronstoff 1983; see review by Sousa 1984). Here we will examine Hutchinson's conjecture by measuring the effect of the intensity and frequency of disturbance on the rate of competitive exclusion, in systems which differ in some of the ways the deep sea and the continental shelf may be hypothesized to differ.

II.3.2 Methods

II.3.2.1 The Model

The model described in this section examines the local results of competition and disturbance. The community is composed of a set of species interacting according to the Lotka-Volterra competition equations

$$dN_i/dt = r_i N_i [K_i - \Sigma \alpha_{ij} N_j]/K_i \qquad (3.1)$$

where K_i is the carrying capacity of species i and α_{ij} is a competition coefficient giving the effect of an individual of species j on the per-capita growth rate of species i. r_i is the hypothetical intrinsic rate of increase of species i under the environmental conditions assumed in (3.1), but with all intra- and inter-specific density effects eliminated.

Given a set of such equations and a set of initial population densities, the community will gradually approach an equilibrium, losing species as it does so. Our focus is on the rate of loss of species, as a function of the parameters in (3.1) and of the frequency and intensity of disturbance (incorporated as described below). To measure the rate of exclusion, replicate simulations of (3.1) were performed. The parameter values (the r_i, K_i and α_{ij}) were sampled from distributions hypothesized to represent the species pool from which members of a community might be drawn.

II.3.2.2 Parameter Values

The communities described by (3.1) were assembled by drawing species randomly from a species pool, defined by the distributions (including means, variances and covariances) from which the r_i, K_i and α_{ij} are drawn. The r_i and K_i were assumed to be lognormally distributed and the α_{ij} normally distributed. Because the difference in generation time between deep sea and shelf populations translates into differences in r_i, we examined species pools with high (0.1) and low (0.01) mean values for r_i. The means for K and α were fixed at 1000 and 1, respectively. Within any species pool, the range of body sizes, trophic and habitat specialization, etc. determines the variances of r, K and α. To examine this effect, the coefficient of variation for r, K and α was set at 0.25 (a species pool composed of very similar species) and 1 (a species pool with a wider range of species types).

As important as the means and variances is the covariance pattern between the parameters. It is commonly hypothesized that r, K and the α_{ij} are not independent, but it is unclear just what pattern

of covariance is to be expected. The most common hypothesis, the basis for the theory of r- and K-selection (MacArthur and Wilson 1967) is that there is a negative correlation between r_i and K_i; species with high rates of increase are more likely to have low carrying capacities and vice versa. The empirical evidence for this pattern is weak at best, so we have examined both positive and negative covariances, and zero covariance as a null case.

The correlation among the parameters is shown in Figure 4 in the form of a path diagram (e.g. Wright 1968, Li 1975). For each pair of species i and j, K_i and K_j are assumed to be indpendent random variables. The carrying capacity of each species is assumed to be correlated with its rate of increase and with both its susceptibility to competition from other species (for species i this is measured by α_{ij}) and its competitive effect on other species (measured by α_{ji}). From these direct correlations, additional correlations are generated between the rates of increase and competition coefficients; these can be derived using the rules of path analysis (e.g. Li 1975).

In our simulations, the correlations a-f in Figure 4 were assigned as follows:

	COV < 0	COV > 0
a	-0.5	0.5
b	-0.5	0.5
c	0.5	-0.5
d	0.5	-0.5
e	-0.5	0.5
f	-0.5	0.5

The negative covariance case (r- and K-selection) assumes that greater resource use efficiency, and thus a higher K, leads to a lower r, less competitive stress from other species, and a greater competitive impact upon other species. The positive covariance case reverses these assumptions. In the zero covariance case, all the correlations are zero, so all the parameters are independent.

II.3.2.3 The Disturbance Process

In this model, disturbance indiscriminately reduces the densities of all species present in the community. It is characterized by its frequency (it is assumed to follow a Poisson process with a specified average frequency of disturbance per unit time) and its intensity (the proportion by which species abundances are reduced).

II.3.2.4 Deep Sea vs. Continental Shelf Contrasts

In terms of the parameters of this model, we expect deep sea and continental shelf communities to differ as follows:

1. Deep sea communities should have a lower average r_i (E(r)) reflecting the lower growth rates and fecundities typical of

deep sea species.

2. The range of parameters, measured in the model by the common coefficient of variation (CV) of r, K and α, is probably smaller in the deep sea than on the shelf. This hypothesis is supported primarily by the much greater range of species abundances found in shelf communities. This variability in abundance is a complex summation of the variability in the species-specific parameter values, and while it is impossible to draw a quantitative relation between the two, the qualitative relation is almost certainly positive.

II.3.2.5 Simulation

For simulation, 20-species communities were established with the parameters drawn from distributions with specified means, variances and covariances. Initial population sizes were set at 100. A third order Runge-Kutta algorithm was used to integrate the equations on an IBM PC microcomputer equipped with an Intel 8087 numeric coprocessor, using 64 bit arithmetic. Extinction times were recorded as species were excluded from the community.

A continuous model like (3.1) permits arbitrarily small population sizes, and thus requires the imposition of an extinction threshold. We chose an extinction threshold of one individual. Since we are not attempting to be quantitatively precise in our predictions of population size, different thresholds are equivalent to different choices of a scale for measuring population density, and should not qualitatively affect our conclusions.

II.3.3 Results

II.3.3.1 Unperturbed Communities

Figure 5 presents a set of species survivorship curves, showing the rate of competitive exclusion in 50 replicate 20-species communities for each set of parameter values. Several conclusions are evident.

First, for at least the first 90% or so of the species which go extinct, the rate of extinction is roughly constant for any parameter combination, as evidenced by the approximate linearity of the survivorship curves on the semi-log plots.

Second, the rate of extinction varies widely as a function of the parameter values. Higher values of r, higher coefficients of variation in the parameters, and more negative covariance patterns between r and K all lead to more rapid rates of species exclusion.

To examine the dependence of extinction time on E(r) and CV more quantitatively, we calculated the median extinction time (i.e. the time at which 50% of the original species had gone extinct; this measures the "life expectancy" of a species at the beginning of the simulation) as a function of E(r) and CV. Figure 6 shows the

effects of E(r), for a coefficient of variation CV=0.5. The data are roughly linear on a log-log plot, with a slope close to -1. Thus, median extinction time is proportional to 1/E(r). In Figure 7 is shown the response to changes in CV, for E(r) fixed at .05. Again the result is close to a power function, with an exponent of -1.

These results predict the relative rates of competitive exclusion in the two habitats. In the deep sea, with its lower values of r and CV, extinction time is predicted to be much longer than is the case on the shelf.

II.3.3.2 Communities Subject to Disturbance

Hutchinson's conjecture predicts that exclusion time will be maximized at an intermediate frequency of disturbance. This frequency should be directly proportional to the rate of exclusion in the absence of disturbance, and (based on the results in the preceeding section) should be lower in the deep sea than on the continental shelf (Figure 8). If this prediction is correct, increasing the frequency of disturbance by additional anthropogenic disturbance is more likely to reduce the diversity of a deep sea community than that of a continental shelf community. To put it another way, in any community there should be a critical frequency of disturbance beyond which further increases in frequency eliminate species. This critical frequency should be lower in the deep sea than on the shelf.

This prediction is, of course, predicated on the correctness of Hutchinson's conjecture. To examine this, we incorporate abiotic disturbance into our model and examine its effects on the rate of competitive exclusion.

These results are shown in Figures 9a-d, in which the median extinction time (i.e. the life expectancy of a species at the beginning of the simulation) is plotted as a function of the frequency of disturbance for different disturbance intensities and all combinations of high and low E(r), high and low CV, and negative, zero and positive COV. The figures plotted are means of ten replicate simulations, ± 1 standard error.

The two black triangles appearing on the abcissa of each graph provide a scale on which to evaluate Hutchinson's conjecture about the relation between the time scales of disturbance and exclusion. The lower triangle marks the frequency corresponding to one disturbance per baseline median extinction time (i.e. per extinction time in the absence of disturbance). The upper triangle is an order of magnitude higher, corresponding to a frequency of 10 disturbances per median extinction time. Thus the range of frequencies between the triangles corresponds to one operational definition of a disturbance operating "on the same time scale" as competitive exclusion. Hutchinson's conjecture predicts that the critical frequency should lie in this interval.

II.3.3.2.1 Effects of the Covariance Pattern

In each of Figures 9a-d, the upper row shows the positive covariance case, the middle row the zero covariance case and the bottom row the negative covariance case. Disturbance significantly extends extinction time only when the covariance between r and K is negative or zero, in which case extinction time can be increased by as much as 100% (Fig. 9c,d). If COV>0, the only effect of disturbance is to speed up extinction.

This pattern can be understood in terms of the dynamics of the species making up the community (Huston 1979). As the populations grow in the absence of disturbance, the first to experience a shortage of resources are those with the lowest values of K, which thus tend to be excluded early. When disturbance reduces the overall density, those species with higher values of r will increase the most rapidly. If they tend to be the species with low values of K, the disturbance will greatly extend their persistence. If r and K are independent, however, the species which benefit from the reduction in density are as likely to be those which are winning as those which are losing in competition, and there will be little or no effect on extinction time. If the covariance is positive, disturbance will usually favor the winning species, and act to speed up exclusion of the losing species.

II.3.3.2.2 Effects of the Coefficient of Variation

Figures 9a,b show the results for CV=1, Figures 9c,d the results for CV=0.25. The coefficient of variation affects both the magnitude of the effect on extinction time and the critical frequency value. The magnitude of the disturbance effect is inversely proportional to CV, as is most apparent when COV<0. Comparing the bottom rows of Figures 9a,b with Figures 9c,d, we see that increasing decreasing CV by a factor of 4 (from 1 to .25) increases the effect of disturbance from about 25% to 100%. When COV=0, there is no observable increase in extinction time when CV=1, and as much as 25% increase when CV=.25.

II.3.3.2.2 Effects of the Average Value of r

Figures 9a,c show the results for E(r)=0.01, Figures 9b,d the results for E(r)=0.1. The effect of disturbance on increasing extinction time is more obvious at low E(r) than at high E(r). The biggest effect of E(r), however, is on the critical frequency at which extinction time is maximized. In absolute terms, the critical frequency is directly proportional to E(r), which supports Hutchinson's conjecture. That is, in communities composed of "slow" species (low E(r)), the critical frequency is lower than in a community of species with higher E(r). When measured in scaled terms (i.e. the scale marked by the black triangles in Figure 9), the critical frequency is roughly independent of E(r). That is, extinction time is maximized by disturbance at some fixed frequency per baseline extinction time.

When COV=0 or COV>0 the frequency at which extinction time begins to decrease is inversely proportional to E(r); i.e. in communities

with lower values of E(r) disturbance begins to decrease extinction time at lower frequencies.

II.3.4 Conclusions

If we compare typical deep sea communities, with low values of E(r) and CV, with shelf communities typified by high values of these parameters, we draw the following conclusions from Figures 5-9:

1. Deep sea communities should have a much lower baseline rate of competitive exclusion in the absence of disturbance.

2. Deep sea communities should show a much greater increase in competitive exclusion time under the impact of disturbances of moderate frequency and intensity.

3. The critical frequency above which additional disturbance speeds up extinction is lower for deep sea communities.

4. When the critical frequency is exceeded in deep sea communities, the decrease in extinction time is more precipitous than in shelf communities. Thus biotic impoverishment generated by too high a frequency of disturbance will be more abrupt in deep sea than in shelf communities.

Whether these results imply that deep sea communities are more or less sensitive to dumping of waste depends on the disturbance regime represented by such dumping. The frequency and intensity of disturbance near the center of a dump site are likely to be so high that the community will be effectively obliterated. Farther away, disturbance will be more intermittent and less intense. Such disturbance might conceiveably decrease the rate of local competitive exclusion, and thus increase diversity (see e.g. the results of Pearson 1980 on benthic community diversity near a toxic effluent source). If the joint action of anthropogenic and natural disturbance raises the frequency above the peak in the curves in Figure 9, however, the result will be just the opposite.

It is tempting to posit that the lower frequency of natural disturbance (see Grassle, this report) in the deep sea implies that there is more room to add anthropogenic disturbance before reaching the critical frequency and the descending limb of the disturbance response. We caution against this, however, because the critical disturbance frequency above which exclusion time decreases is itself inversely related to the rate of extinction in the absence of disturbance. It is probably not possible to predict where on the curves of Figure 9 a typical deep sea or continental shelf community is likely to lie without experimental study of the effects of disturbance frequency.

This model examines only local extinction time. Spatial heterogeneity is conspicuous only by it absence. In a spatially heterogeneous environment, local extinction of the sort described by this model is balanced against colonization from other

locations. In the next section, we present some results of an even more abstracted model which examines this balance and its results on coexistence and diversity. Local competitive exclusion, which is the dependent variable in the model of this section, appears as a parameter in the next model.

II.4. A Spatially Heterogeneous Community Model

II.4.1 Background

Regional nonequilibrium coexistence in a spatially heterogeneous environment depends on the relation between the time scale of local interactions, the rate of dispersal between patches, and the rate of creation of new patches by disturbance (Caswell 1978, Sousa 1984). Such community properties as local species richness ("alpha diversity"), spatial heterogeneity ("beta diversity"), species-area or rarefaction curves and association patterns are the result of the interaction of these parameters.

II.4.2 Methods

II.4.2.1 The Model

The spatially homogeneous model of the previous section describes the local dynamics following colonization of a newly created patch. In principle, it would be possible to construct a model of an ensemble of such patches, each described by the model in Section 3, and to couple them by a description of colonization. However, such a model would be extremely complicated and contain far more detail in its parameters than could be interpreted. Instead, we have abstracted the processes described in that model to focus on the time scale of competitive exclusion within patches, and to examine this time scale in relation to the time scales of disturbance and colonization.

We consider a community which occupies a large but finite set of patches or 'cells', and further simplify the community to consist of two competing species. These two species may equally well be thought of as representing two competing guilds or functional groups of species. Within each patch we note only the presence or absence of a species, so the model contains no local density information. Regional abundance of a species is given by its frequency of occurrence.

Our model describes the dynamics of this community by a nonlinear Markov chain similar to but more general than those considered by Horn (1975), Usher (1979) and Abugov (1982). A more detailed description of the model and its implications in in preparation (Caswell and Cohen, in prep.). The state of a typical cell is specified by the presence or absence of each of a set of species. For n species, there are 2^n possible states. These states can be conveniently numbered from 0 to 2^n-1 by their binary expansions. For the two species case, where 0 denotes absence and 1 presence, the 4 cell states are:

Sp.1	Sp2	State
0	0	0

0	1	1
1	0	2
1	1	3

At any given time, the state of the collection of cells is given by the vector $\underline{p}(t)$, the elements of which give the frequency distribution of cell states. The transition probabilities between those states depend on the species interactions, dispersal, and environmental variability. These transitions specify a Markov process:

$$\underline{p}(t+1) = \underline{A}_t \underline{p}(t)$$

where the (i,j) entry of the transition matrix $\underline{A}_t$ gives the probability of transition from state j to state i. Since $\underline{A}_t$ depends on the current state distribution, it is a nonlinear Markov process, to which much of standard stochastic process theory does not apply.

In our considerations of competitive communities, we assume that Species 1 is the loser and Species 2 the winner in the competitive interaction within a cell. The possible state transitions in the simplest such system are given by the graph and matrix in Figure 10, where:

π_d = the probability of disturbance
C_i = the probability of colonization by species i
π_c = the probability of competitive exclusion (i.e. that a cell containing both species will complete the competitive exclusion process in the next time unit).

Each of these parameters is defined in terms of more detailed biological and environmental processes. Environmental disturbances are assumed to follow a Poisson process with a mean frequency of disturbance per unit time given by f, so that

$$\pi_d = 1 - \exp(-f) \qquad (4.1)$$

Colonization is also assumed to follow a Poisson process, with an average frequency of colonization proportional to the product of the number of cells occupied by the species in question (F_i) and a dispersal coefficient (D_i) which measures the combined effects of the production of offspring and their survival to colonization. A first approximation to the colonization probability is then given by

$$C_i = 1 - \exp(-D_i F_i) \qquad (4.2)$$

However, if a disturbance of the sort of interest here occurs at the same time as the arrival of a propagule, it will effectively prevent colonization. Thus we can use

$$C_i = (1-\pi_d)(1-\exp(-D_i F_i) \qquad (4.3)$$

as a more realistic description of colonization probability.

The probability of competitive exclusion depends on the time required for exclusion within a cell, denoted by TC. The simplest model assumes that in any time unit 1/TC of the cells containing both species should collapse back to state 1, so that

$$\pi_c = TC^{-1} \qquad (4.4)$$

However, in the presence of disturbance this overestimates the fraction of cells containing both species that will be ready to go extinct, because some of the "older" cells (i.e. those in which the two species have been coexisting for the longest time) will have been eliminated by disturbance. We can take the age distribution of patches into account (Caswell and Cohen, in preparation) by setting

$$\pi_c = [\exp(-fTC)-\exp(-fTC+f)]/[\exp(-fTC)-1]. \qquad (4.5)$$

Disturbances produce empty cells, which can be colonized by either or both of the competitors. Once a cell has been colonized by the winner (Species 2) it is unavailable for colonization by the loser. The winner, on the other hand, can colonize cells occupied by the loser: when it does so, competition eventually eliminates the loser.

This description of disturbance and colonization assumes that a disturbed cell is immediately available for colonization. While this is true for many classes of natural disturbance, it may not be so for anthropogenic disturbance involving toxic wastes. To model disturbances which not only eliminate species but also leave residual toxic effects that prevent colonization, we add a fifth, "poisoned" state to the system:

Sp.1	Sp2	Residual Effect	State
0	0	0	0
0	1	0	1
1	0	0	2
1	1	0	3
0	0	1	4

and change the transition diagram as shown in Figure 11. The probability that a cell in state 5 recovers to the colonizable state 0 depends on the time required for recovery, TR. By analogy with (4.5), we set

$$\pi_r = [\exp(-fTR)-\exp(-fTR+f)]/[\exp(-fTR)-1]. \qquad (4.6)$$

II.4.2.2 Analysis

Given any initial distribution of cell states, the system described by (4.1) eventually converges to a limiting probability distribution $\underline{p}$. This distribution corresponds to a community

pattern characterized by a certain proportion (p_0) of empty cells, a certain proportion (p_1 and p_2) of cells containing each species by itself, and a certain proportion (p_3) of cells containing both species, coexisting temporarily before Species 2 excludes Species 1. We have written a computer program to solve for this distribution numerically. The program was implemented on an IBM PC microcomputer with an Intel 8087 numeric coprocessor, using 64 bit arithmetic.

As dependent variables we have calculated the following quantities from the vector $\underline{p}$:

1. The frequency of occurrence (F_i) of each of the species, given by

$$F_1 = p_2 + p_3$$
$$F_2 = p_1 + p_3$$

2. Local species diversity ('alpha diversity'), calculated as the expected number of species found in a randomly selected patch:

$$\alpha = p_1 + p_2 + 2p_3$$

3. Community heterogeneity (or 'beta diversity'), measured as the entropy of the vector $\underline{p}$:

$$\beta = -\Sigma p_i \log(p_i)$$

We examined these variables as they respond to changes in

1. The time required for competitive exclusion (TC)
2. The dispersal coefficients (D_i) of the two species.
3. The frequency of disturbance (f).
4. The time required for recovery from the residual effects of disturbance (TR).

II.4.3 Results

II.4.3.1 Disturbances Without Residual Effects

We consider first disturbances which leave no residual effects. Figure 12 shows the effects of disturbance on Species 1, the losing competitor. Recall that in the absence of disturbance this species is totally excluded by Species 2; such a species can obviously rely on an intermediate frequency of disturbance for coexistence. The positive effect of disturbance is greater when TC is large and when dispersal rates are high (Figure 12a-d). As dispersal rates decline, the positive effects of disturbance are seen only at long exclusion times (Figure 12b) and when they are low enough, the positive effects disappear completely (Figure 12a). It is frequently the case that inferior competitors have

evolved increased dispersal capabilities. Such a negative correlation between dispersal and competition definitely increases coexistence (Figure 12e-f), even for low absolute magnitudes of dispersal ability and competitive exclusion time.

The effects of disturbance on the winning competitor are much less interesting (Figure 13). Since Species 2 is by hypothesis unaffected by Species 1, neither competitive exclusion time nor the dispersal rate D_1 has any effect. Instead, a winning species is eliminated by disturbance at a rate which inversely proportional to its dispersal abilities.

The community parameter most frequently considered in pollution studies is diversity. We consider here two measures of diversity: species richness or "alpha diversity", measured as the expected number of species to be found in a randomly selected cell, and spatial heterogeneity or "beta diversity", measured by calculating the Shannon-Wiener diversity index over the vector $\underline{p}$.

Figure 14 shows results for species richness. At sufficiently low dispersal rates, disturbance leads to a monotonic decline in richness (Figure 14a). At higher dispersal rates, communities with high TC values begin to show species richness maxima at intermediate disturbance frequencies. For long exclusion times, these increases can be dramatic, with almost every patch containing both species, even though such coexistence is unstable and temporary. When the losing competitor has an edge in dispersal ability (Figure 14e-f) the intermediate diversity maximum is exhibited even when the losing competitor has a low dispersal rate.

The response of beta diversity to disturbance is complex (Figure 15), because it reflects several different changes in the distribution of cells among the four possible states of the system. At low dispersal rates, beta diversity increases until an intermediate frequency, and then drops off essentially to zero as both species become largely extinct (cf. Figs. 12a, 13a and 15a). At higher dispersal rates (Fig. 15b) beta diversity exhibits a maximum at intermediate disturbance frequencies, with the greatest increase occurring in communities with long competitive exclusion times. At higher dispersal rates, or when the correlation between dispersal and competitive ability is negative, the pattern depends strongly on TC: both intermediate maxima and a bimodal pattern with two maxima are exhibited. The one conclusion that can be drawn from these results is that a certain amount of disturbance will tend to increase the spatial complexity of a community, but that too much disturbance eventually leads to a community monotonous in both species richness and spatial heterogeneity.

How do these results relate to the comparison of the deep sea and the shelf? Deep sea communities are characterized by longer competitive exclusion times (this follows from the models of the previous section), by lower natural disturbance frequencies, and by lower dispersal and colonization rates. These contrasts leave our predictions about increased disturbance frequencies ambiguous.

The lower dispersal rates imply that deep sea communities are more likely to respond to disturbance by reduced species abundance and diversity. The longer competitive exclusion times, on the other hand, imply the opposite, and also suggest that the higher natural diversity of deep sea communities could be supported even by the lower rate of natural disturbance, since increasing TC shifts the peak in the species richness graph to lower disturbance frequencies.

In any case, the results of adding a new form of disturbance to such a community depend on whether the natural disturbance frequency lies above or below that critical intermediate frequency at which species richness is maximized. In systems with larger values of TC the critical frequency is lower, implying that their tolerance for increases in disturbance frequency is less.

II.4.3.2 The Importance of Residual Effects

The impact of the residual effects of disturbance is shown in the next series of figures. High enough disturbance frequencies produce deserts, with no cells available for colonization (Figure 16a). The rate at which p_4 approaches 1 depends on the recovery time TR; the larger is TR the less disturbance the system can stand. The effects of disturbance on the Species 2 (Figure 16b) are similarly intensified by longer recovery times. Neither of the patterns in Figure 16 depend on the dispersal rates or the competitive exclusion times.

The effects of disturbance and recovery on the losing competitor are shown in Figure 17, which shows all combinations of high and low dispersal rates and competitive exclusion times. In each case, Species 1 is more abundant when recovery is rapid; when TR=100, Species 1 is found only when high dispersal rates combine with slow competitive exclusion, and then only at low disturbance frequencies. The most interesting contrast for our purposes is between the case with low dispersal and slow competitive exclusion (the deep sea) and the case with high dispersal rates and rapid exclusion (the shelf). The patterns are nearly identical (Fig. 17b-c), suggesting that these two differences between the two habitats very nearly cancel themselves out.

Species richness (Figure 18) shows a similar pattern. Again the deep sea and shelf results are nearly identical (Figure 18b-c). Disturbance has its most dramatic positive effects on diversity when dispersal is high and exclusion slow (Fig. 18d), and has no positive effects when dispersal is low and exclusion fast (Fig. 18a).

From Figure 18 it is apparent that the effect of increasing TR is to reduce the positive effects of disturbance and to shift the critical frequency, if there is one, to the left. The rate of recovery from initial disturbance to a state suitable for colonization depends on the rate of sedimentation and the metabolic rate of the microbial community. Both these processes are slower in the deep sea, so deep sea communities are very

likely characterized by higher TR values. If this is so, anthropogenic disturbance in the deep sea is more likely to result in biotic impoverishment than is such disturbance in shallow water.

II.5. Overall Conclusions

1. There is no immediately applicable body of theory with which to evaluate the relative sensitivity of deep sea communities on the basis of their diversity alone.

2. Demographic sensitivity to changes in life history parameters is, in general, positively correlated with population growth rate and negatively correlated with juvenile survival, time to maturity and fecundity. Since deep sea populations are characterized by longer time to maturity, lower fecundity and (although this is less certain) decreased juvenile survival, no unambiguous prediction of their sensitivity relative to shelf populations can be made from this model.

3. In the absence of disturbance, the time required for local competitive extinction is inversely proportional to the average intrinsic rate of increase (E(r)) in the community and to the inter-population variance in population parameters (CV). Since deep sea communities have lower values of both E(r) and CV, baseline extinction times in the deep sea should be much longer than on the shelf.

4. If the correlation between carrying capacity and intrinsic rate of increase is negative, disturbance can greatly extend the time required for local competitive exctinction. The magnitude of this effect is inversely proportional to CV. The greatest extension of extinction time occurs at an intermediate "critical frequency" of disturbance. This critical frequency is inversely proportional to E(r). Above the critical frequency disturbance dramatically reduces extinction time. This reduction is most precipitous in communities characterized by low E(r) and low CV. Thus disturbance in the deep sea has a greater potential to extend local persistence, but deep sea communities should be more sensitive to exceeding the critical frequency and the critical frequency itself is lower. No unambiguous prediction of the overall relative sensitivity to disturbance can be made.

5. In spatially heterogeneous environments characterized by a balance between local extinction and recolonization, local species richness is maximized at intermediate disturbance frequencies. The critical frequency is inversely proportional to the time required for local competitive exclusion. The magnitude of the peak in diversity is directly proportional to dispersal rates and to the time required for local competitive extinction. Since deep sea communities are characterized by longer local competitive extinction times but lower dispersal rates, it is impossible to predict unambiguously their relative sensitivity to disturbance frequency.

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Figure Captions: Section II

Figure 1. The basic life cycle graph used in population sensitivity calculations. Stage 1 represents newborn individuals, stage 2 reproductively mature individuals. P_1=probability of survival to reproductive maturity, P_2=adult survival, F=adult fecundity, α=time required to reach reproductive maturity.

Figure 2. Frequency distribution of λ, the intrinsic rate of increase, in 1000 life cycles whose parameters were sampled from the distributions specified in the text.

Figure 3. The regression coefficients relating demographic sensitivity to the life cycle parameters in the model (2.5) or, for $\partial\lambda/\partial\alpha$, (2.6).

Figure 4. A path coefficient diagram (Li 1975) showing the correlation patterns among the parameters defining the competition model (3.1). The letters on the arrows refer to the correlation coeffcients, the restrictions listed in the figure guarantee that all correlations are between 0 and 1, and the derived correlations are the result of the assumed pattern and values assumed for coefficients a-f.

Figure 5. The rate of loss of species from initial 20-species communities assembled as described in the text. The curves are derived from 50 replicate runs at each parameter combination. The dots on the curves do not indicate the data points (the curves are essentially continuous), but rather mark off the curves into equal logarithmic intervals.

Figure 6. The median extinction time of a species in a 20-species assemblage as a function of the average value of r_i in (3.1), with the coefficient of variation fixed at CV=0.5.

Figure 7. The median extinction time of a species in a 20-species assemblage as a function of the coefficient of variation of the parameters in (3.1), with the $E(r_i)$ fixed at .05.

Figure 8. The predicted effect of disturbance frequency on exclusion time, based on Hutchinson's conjecture, for communities with low (a) and high (b) inherent rates of exclusion in the absence of disturbance.

Figure 9(a-d). The median extinction time (mean ± SE, 10 replicates) as a function of disturbance frequency and intensity, for communities characterized by high and low values of the average rate of increase (E(r)) and the coefficient of variation (CV, which equals 1.0 unless explicitly indicated as CV=0.25 on the graph) of the

parameters r_i, K_i and $\alpha_{i,j}$ in (3.1), and by negative, zero and positive values of the covariance (COV) of r_i and K_i.

Figure 10. The transition graph and matrix for the markov chain model for 2 competing species subject to disturbance.

Figure 11. As in Figure 10, but with the addition of a 5th state corresponding to cells which have been disturbed but are not available for colonization due to the residual effects of the disturbance.

Figure 12. The frequency (F[1]) of the losing species as a function of disturbance frequency and competitive exclusion time (TC), for the 2-species model without residual effects. D[i] is the dispersal coefficient for species i.

Figure 13. The frequency (F[2]) of the winning species as a function of disturbance frequency and competitive exclusion time (TC), for the 2-species model without residual effects. D[i] is the dispersal coefficient for species i.

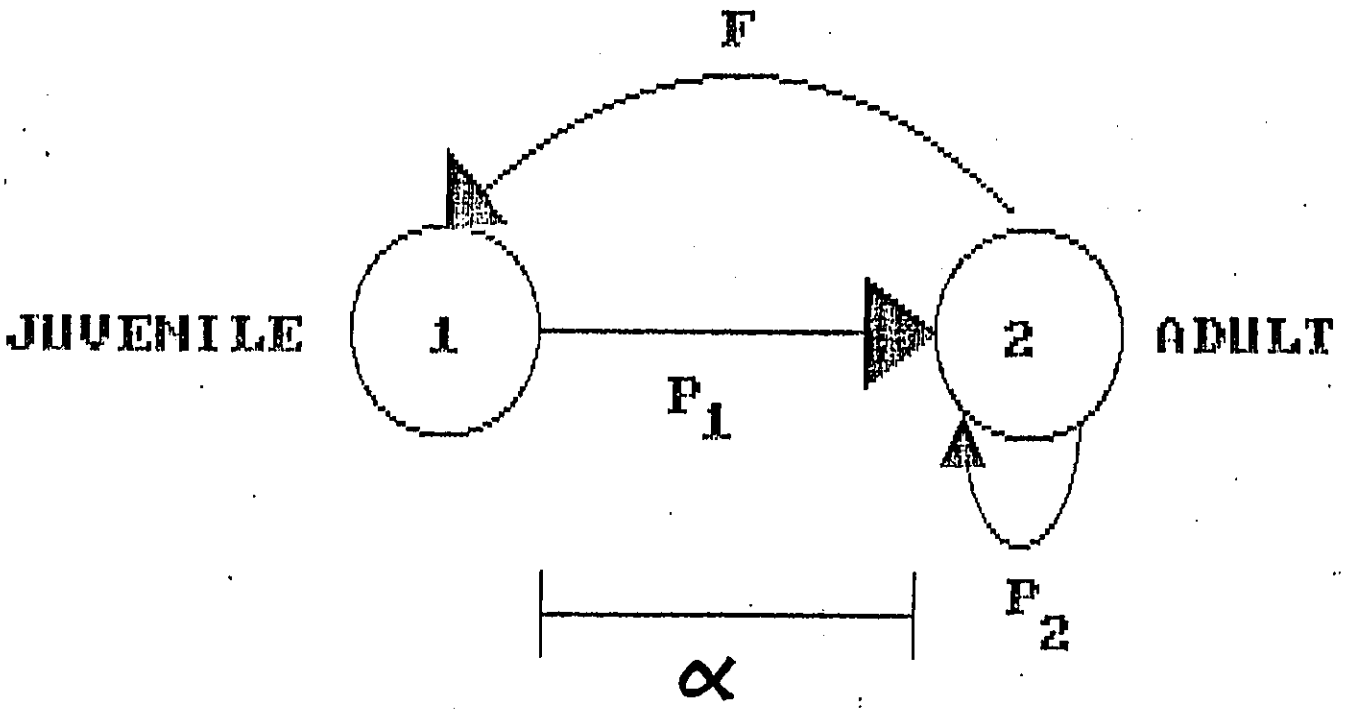
Figure 14. Average species richness in the 2-species model without residual effects, as a function of disturbance frequency and competitive exclusion time.

Figure 15. Spatial heterogeneity or beta diversity in the 2-species model without residual effects.

Figure 16. The results for P[4], the proportion of cells in the uncolonizable state 5 and for F[2], the frequency of occurrence of the winning competitor as a function of disturbance frequency and the time (TR) required for recovery of a disturbed cell to the colonizable state (state 0). Examples are shown for D[1]=D[2]=10, TC=100; other parameter values have little or no effect on the pattern and are not shown.

Figure 17. The frequency (F[1]) of the losing species as a function of disturbance frequency and the time (TR) required for recovery. Results are shown for high and low dispersal (a and b vs. c and d) and for short and long competitive exclusion times (a and c vs. b and d).

Figure 18. Expected species richness as a function of disturbance frequency and the time required for recovery. Parameter values as in Figure 17.


F
JUVENILE
1
2
ADULT
F_1
F_2
α

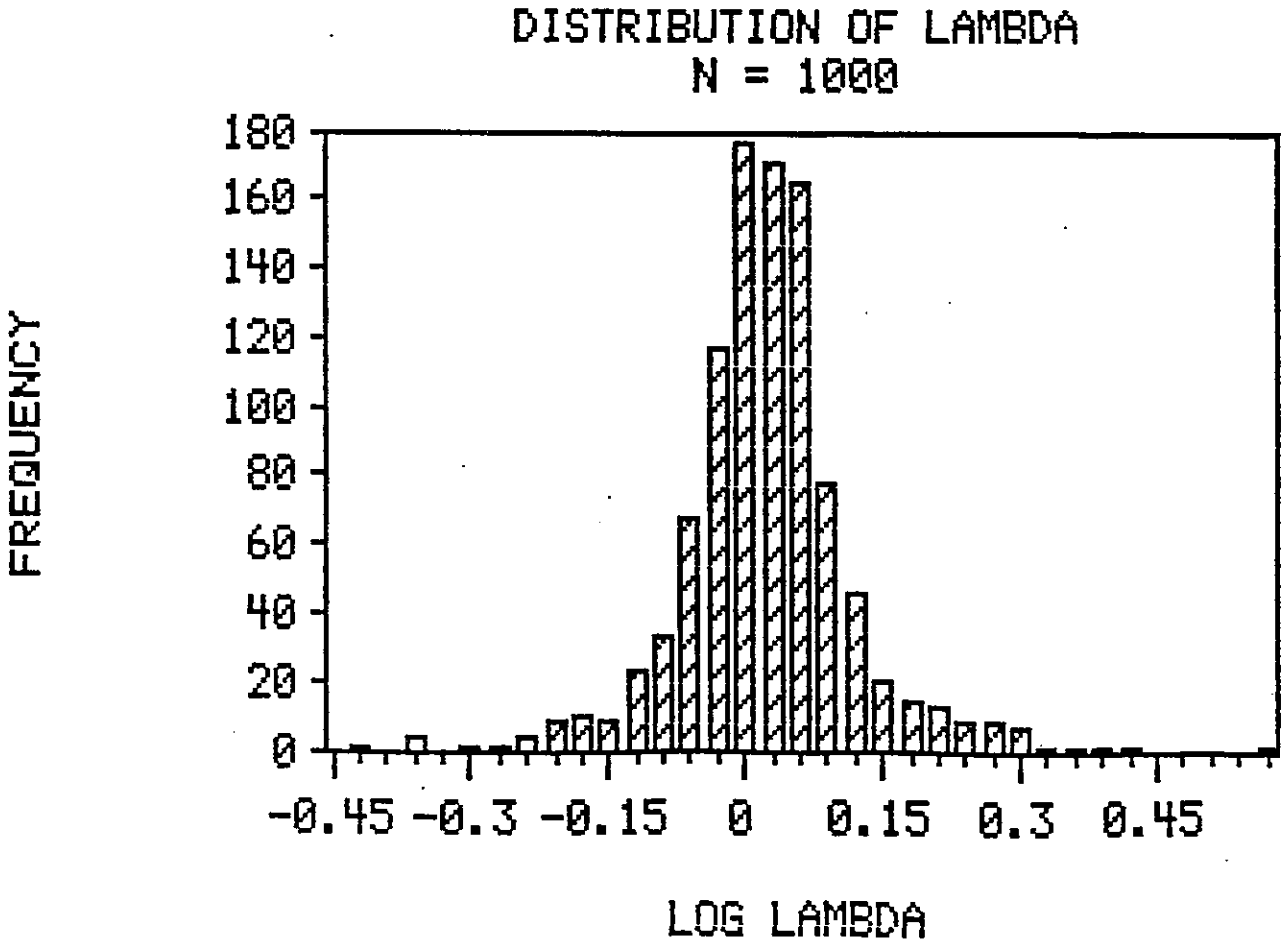
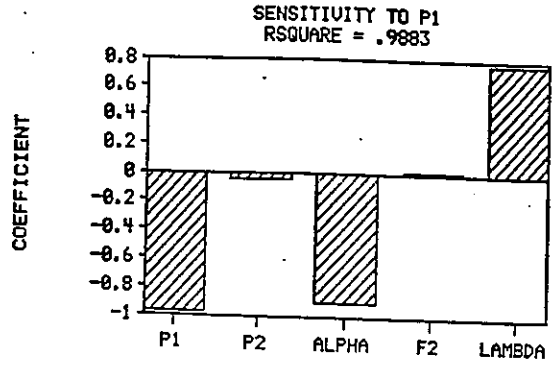
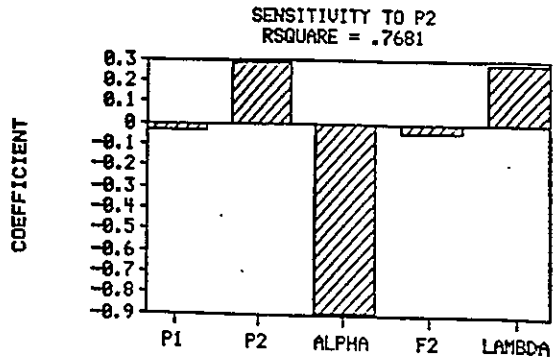
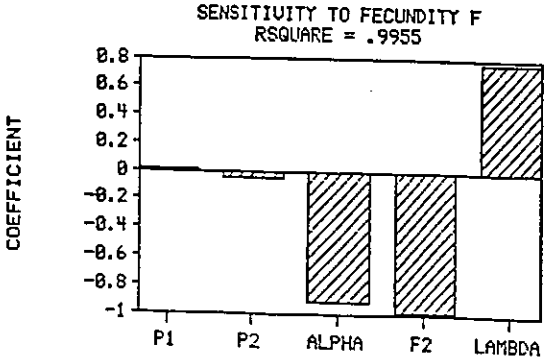
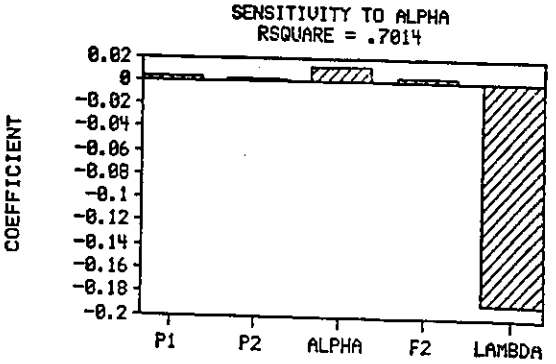

DISTRIBUTION OF LAMBDA
N = 1000
FREQUENCY
180
160
140
120
100
80
60
40
20
0
-0.45
-0.3
-0.15
0
0.15
0.3
0.45
LOG LAMBDA

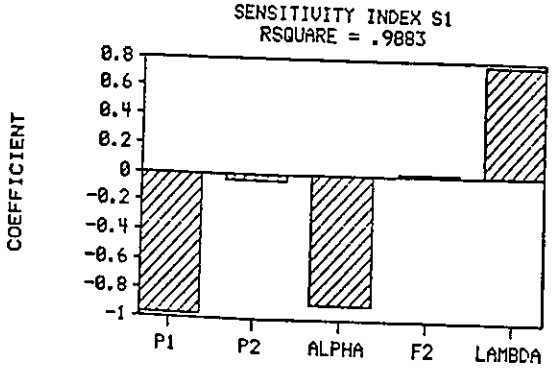
Fig 2


SENSITIVITY TO P1
RSQUARE = .9883
COEFFICIENT
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P1
P2
ALPHA
F2
LAMBDA


SENSITIVITY TO P2
RSQUARE = .7681
COEFFICIENT
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
-0.9
P1
P2
ALPHA
F2
LAMBDA


SENSITIVITY TO FECUNDITY F
RSQUARE = .9955
COEFFICIENT
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P1
P2
ALPHA
F2
LAMBDA


SENSITIVITY TO ALPHA
RSQUARE = .7014
COEFFICIENT
0.02
0
-0.02
-0.04
-0.06
-0.08
-0.1
-0.12
-0.14
-0.16
-0.18
-0.2
P1
P2
ALPHA
F2
LAMBDA


SENSITIVITY INDEX S1
RSQUARE = .9883
COEFFICIENT
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P1
P2
ALPHA
F2
LAMBDA

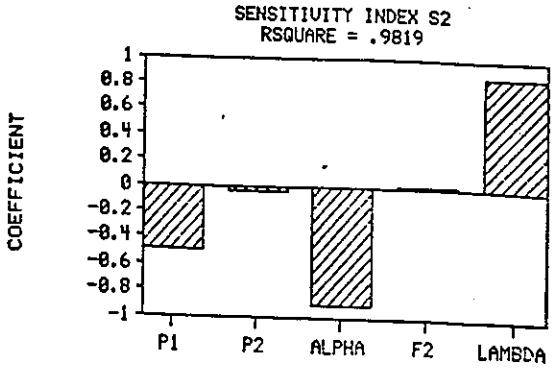
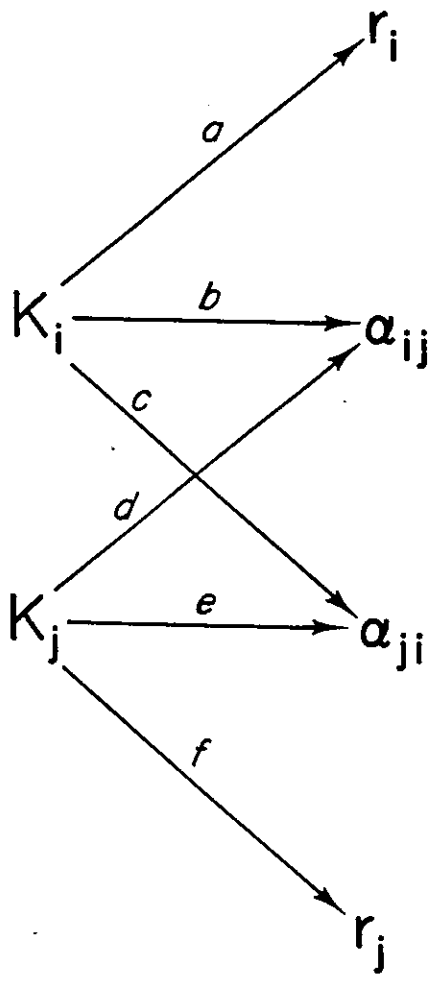

SENSITIVITY INDEX S2
RSQUARE = .9819
COEFFICIENT
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
P1
P2
ALPHA
F2
LAMBDA

Fig 3



RESTRICTIONS

$-1 \leq a, f \leq 1$

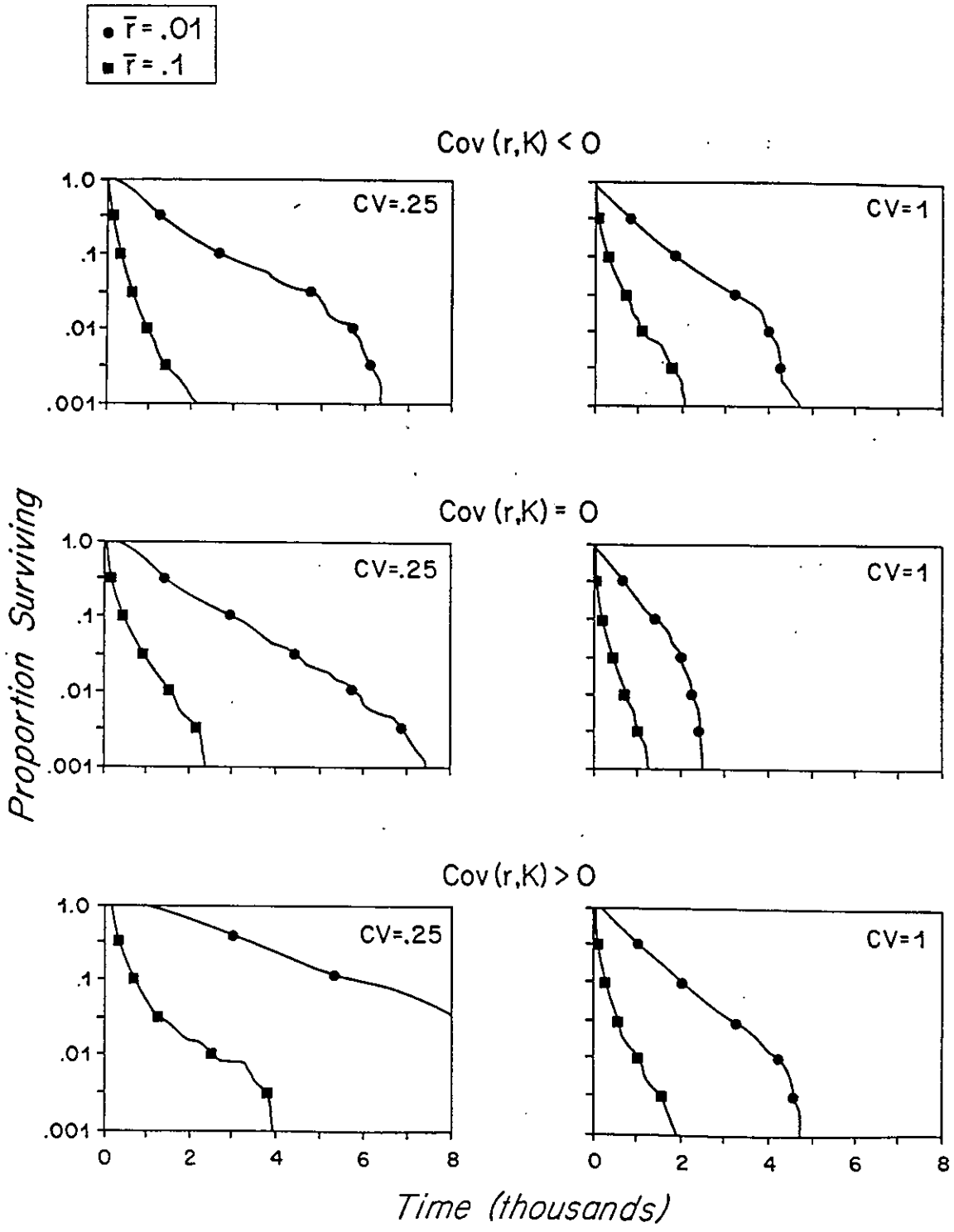
$b^2 + d^2 \leq 1$

$c^2 + e^2 \leq 1$

INDUCED CORRELATIONS

$r_i - \alpha_{ij}$	ab
$r_i - \alpha_{ji}$	ac
$r_j - \alpha_{ij}$	df
$r_j - \alpha_{ji}$	ef
$\alpha_{ij} - \alpha_{ji}$	$bc + de$

Fig 4


● r̄ = .01
■ r̄ = .1
Cov (r,K) < 0
Cov (r,K) = 0
Cov (r,K) > 0
CV=.25
CV=1
1.0
.1
.01
.001
Proportion Surviving
0
2
4
6
8
Time (thousands)

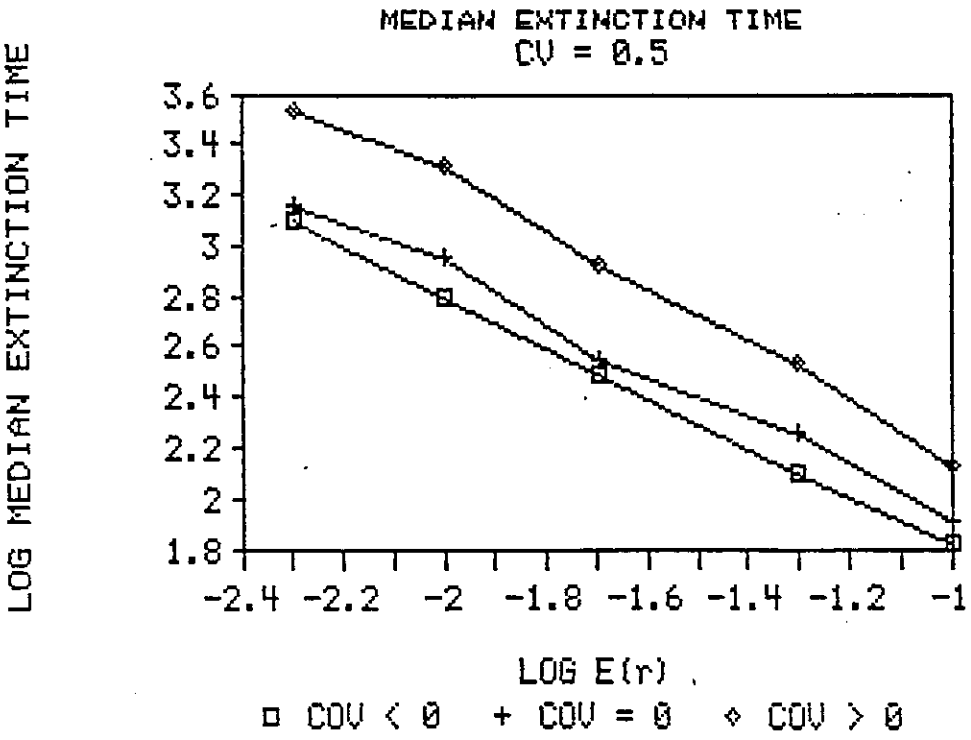

MEDIAN EXTINCTION TIME
CV = 0.5
LOG MEDIAN EXTINCTION TIME
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
1.8
-2.4 -2.2 -2 -1.8 -1.6 -1.4 -1.2 -1
LOG E(r)
□ COV < 0 + COV = 0 ◇ COV > 0

Fig 6

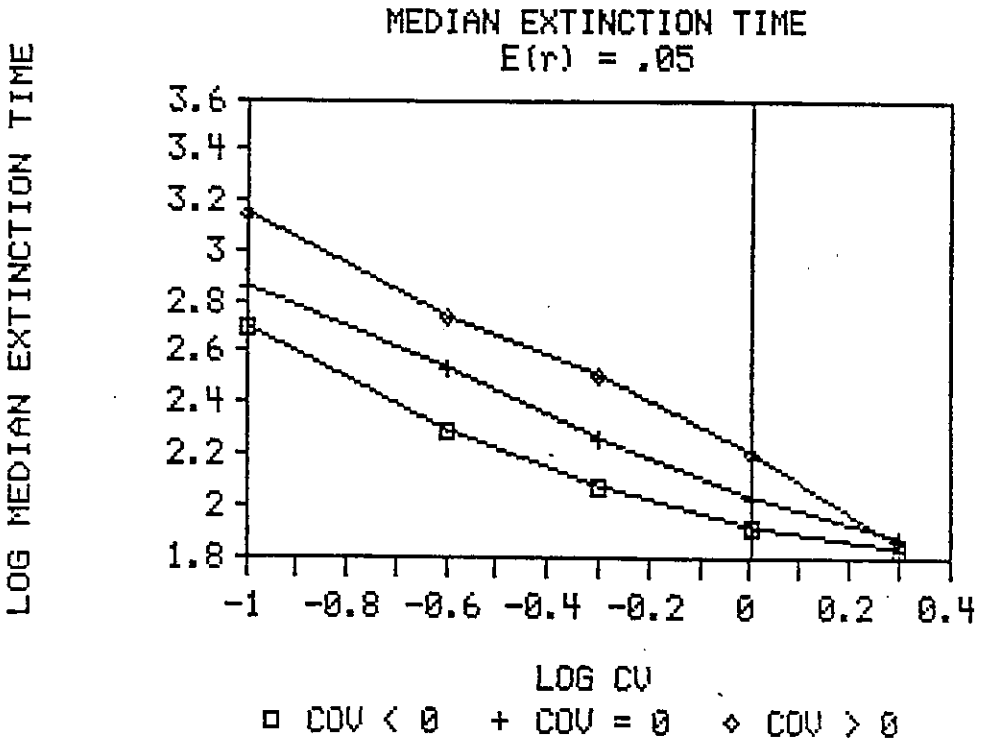

MEDIAN EXTINCTION TIME
E(r) = .05
LOG MEDIAN EXTINCTION TIME
3.6
3.4
3.2
3
2.8
2.6
2.4
2.2
2
1.8
-1
-0.8
-0.6
-0.4
-0.2
0
0.2
0.4
LOG CV
□ COV < 0
+ COV = 0
◇ COV > 0

Fig 2

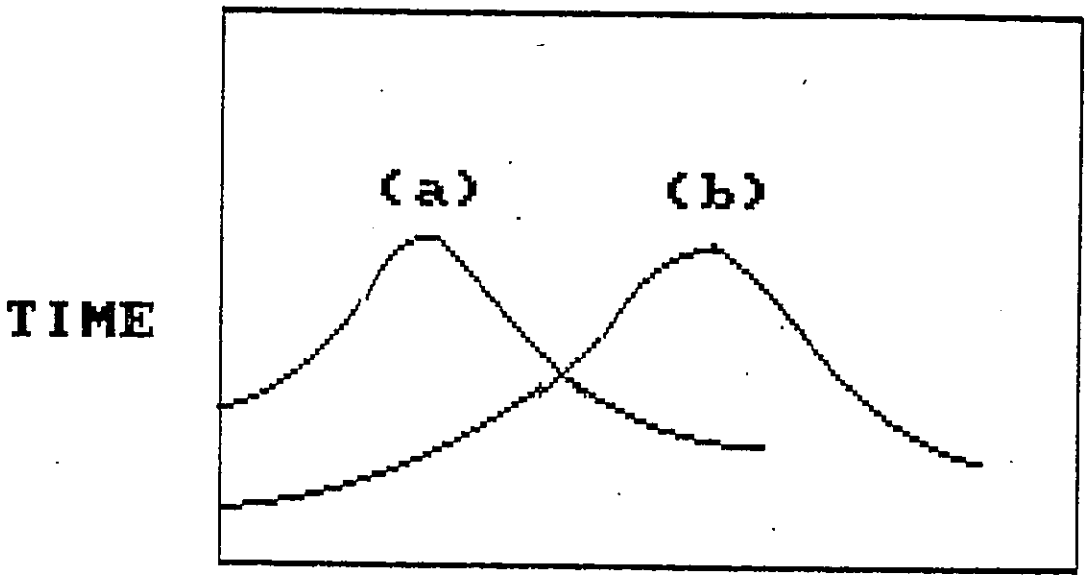
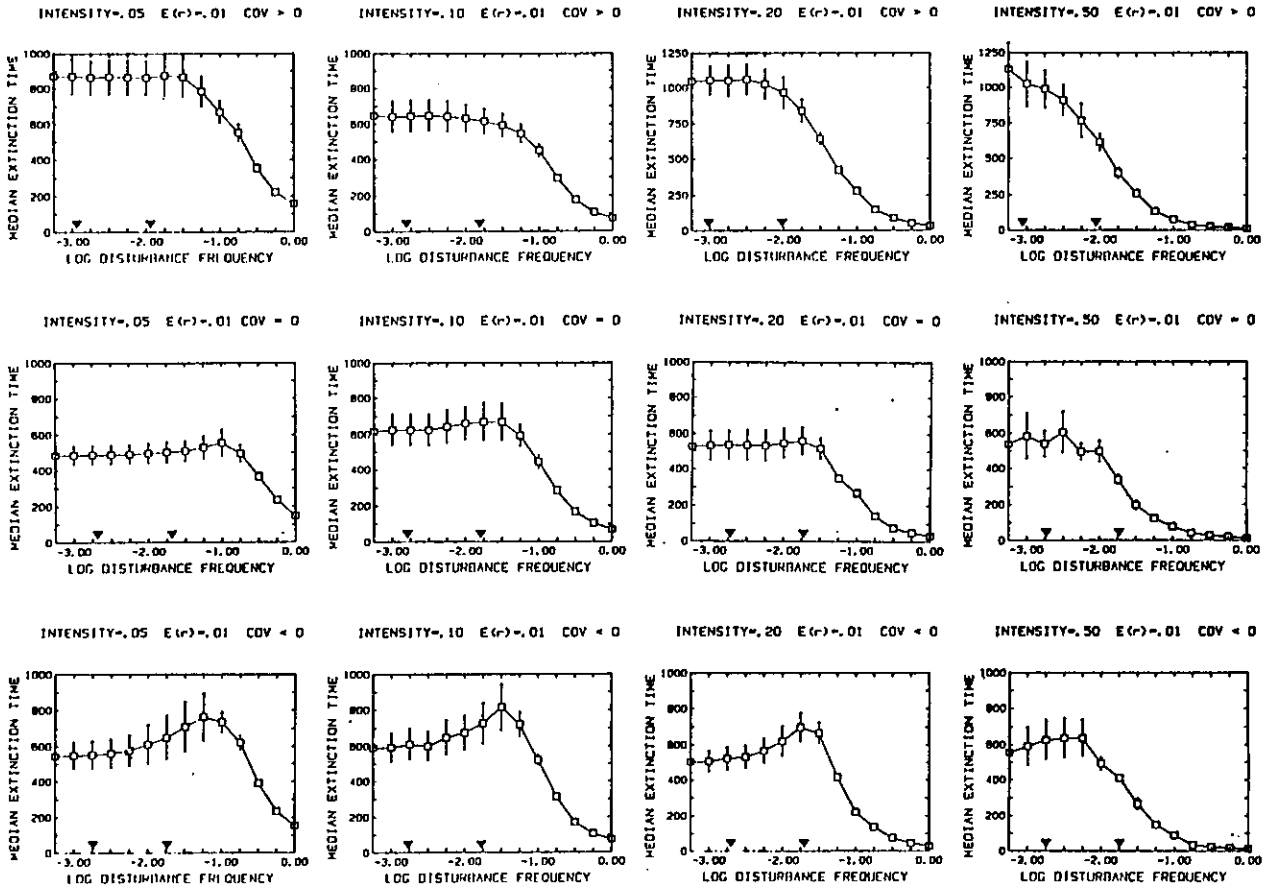
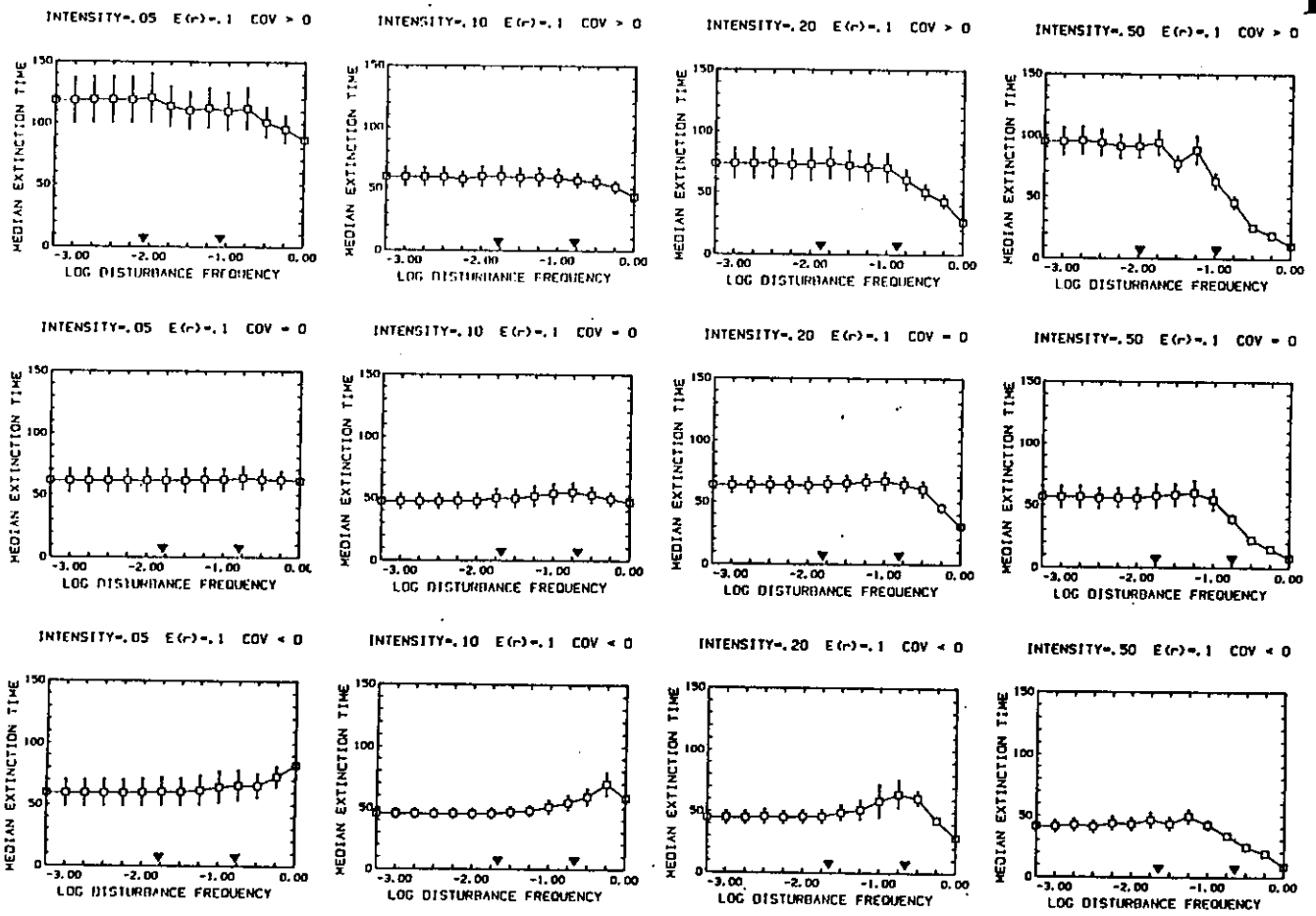


Fig 8

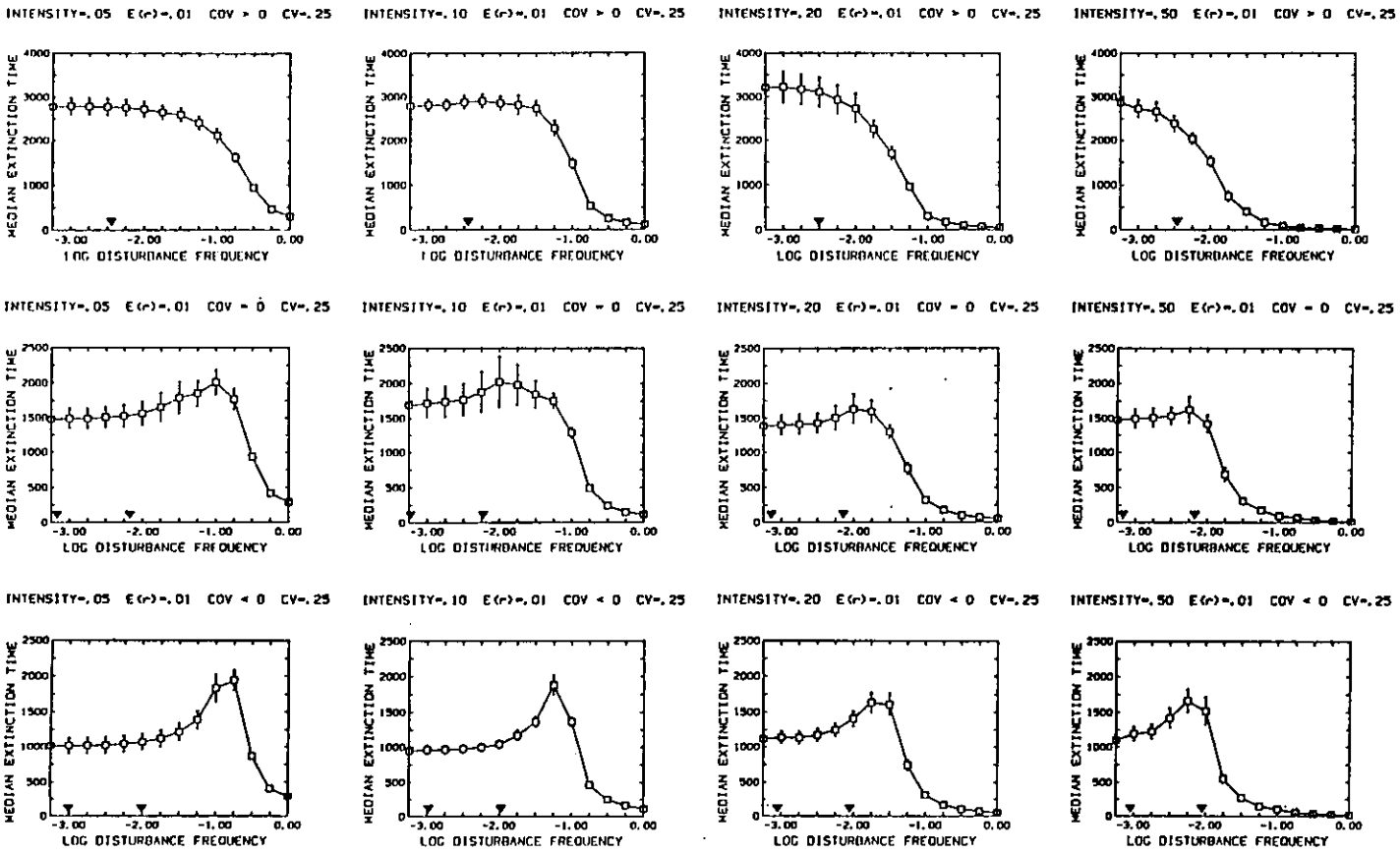
A


INTENSITY=.05 E(r)=.01 COV > 0
INTENSITY=.10 E(r)=.01 COV > 0
INTENSITY=.20 E(r)=.01 COV > 0
INTENSITY=.50 E(r)=.01 COV > 0
INTENSITY=.05 E(r)=.01 COV = 0
INTENSITY=.10 E(r)=.01 COV = 0
INTENSITY=.20 E(r)=.01 COV = 0
INTENSITY=.50 E(r)=.01 COV = 0
INTENSITY=.05 E(r)=.01 COV < 0
INTENSITY=.10 E(r)=.01 COV < 0
INTENSITY=.20 E(r)=.01 COV < 0
INTENSITY=.50 E(r)=.01 COV < 0
MEDIAN EXTINCTION TIME
LOG DISTURBANCE FREQUENCY

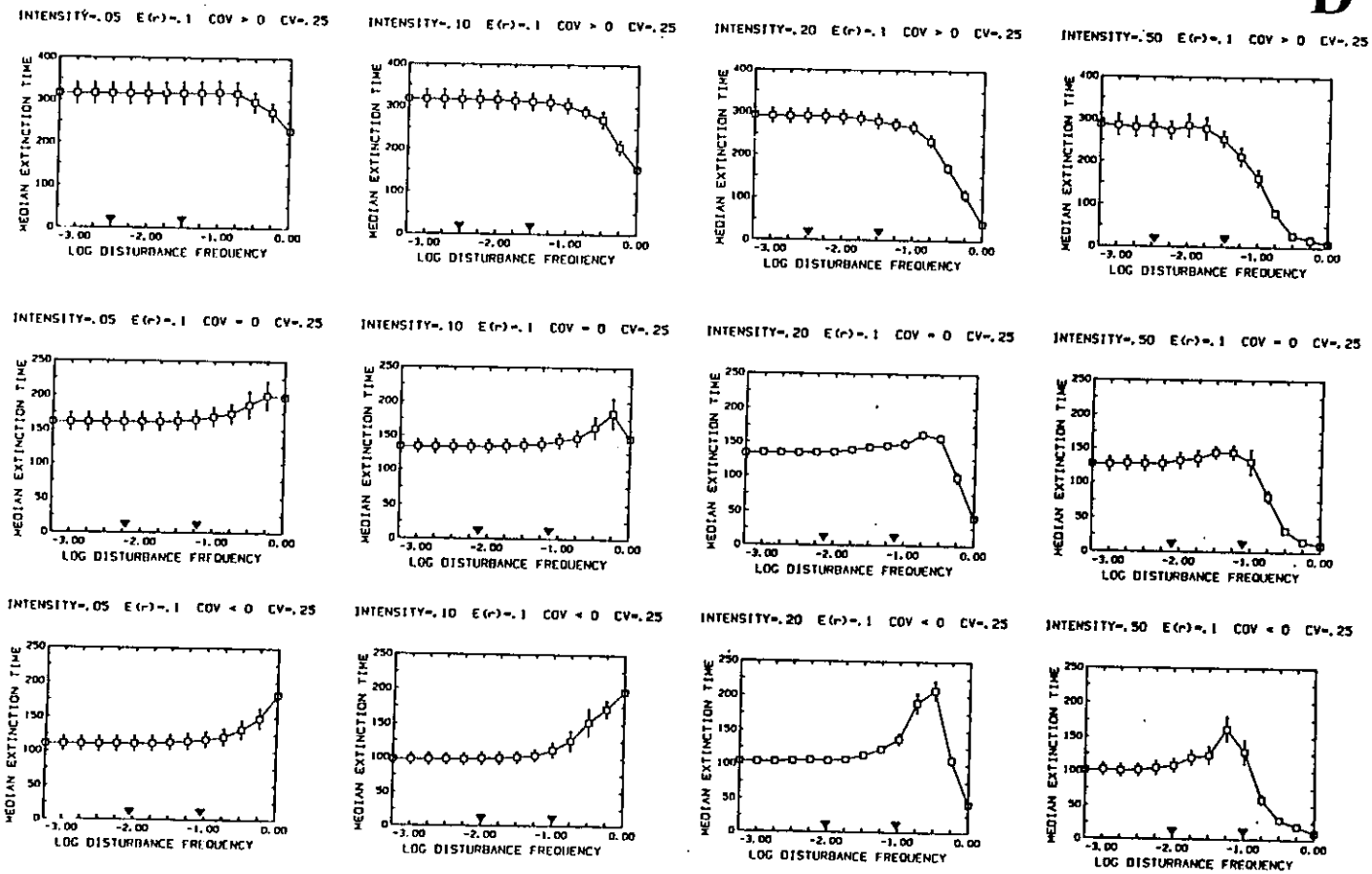
B

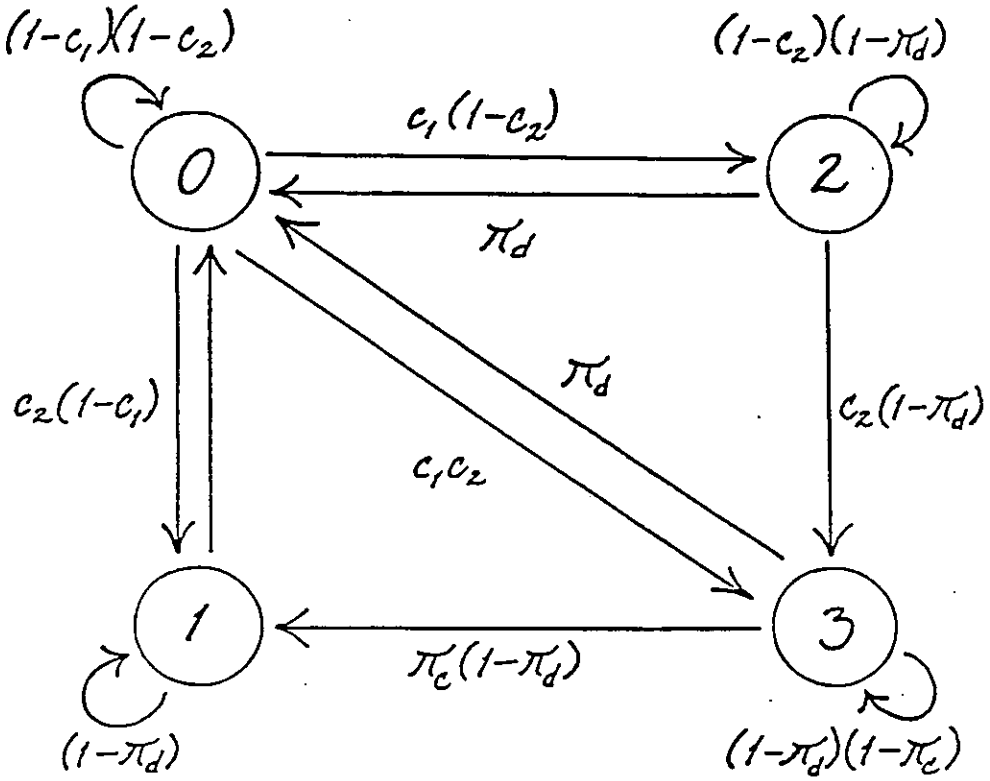

INTENSITY=.05 E(r)=.1 COV > 0
INTENSITY=.10 E(r)=.1 COV > 0
INTENSITY=.20 E(r)=.1 COV > 0
INTENSITY=.50 E(r)=.1 COV > 0
INTENSITY=.05 E(r)=.1 COV = 0
INTENSITY=.10 E(r)=.1 COV = 0
INTENSITY=.20 E(r)=.1 COV = 0
INTENSITY=.50 E(r)=.1 COV = 0
INTENSITY=.05 E(r)=.1 COV < 0
INTENSITY=.10 E(r)=.1 COV < 0
INTENSITY=.20 E(r)=.1 COV < 0
INTENSITY=.50 E(r)=.1 COV < 0
MEDIAN EXTINCTION TIME
LOG DISTURBANCE FREQUENCY
0
50
100
150
-3.00
-2.00
-1.00
0.00

C


INTENSITY=.05 E(r)=.01 COV > 0 CV=.25
INTENSITY=.10 E(r)=.01 COV > 0 CV=.25
INTENSITY=.20 E(r)=.01 COV > 0 CV=.25
INTENSITY=.50 E(r)=.01 COV > 0 CV=.25
INTENSITY=.05 E(r)=.01 COV = 0 CV=.25
INTENSITY=.10 E(r)=.01 COV = 0 CV=.25
INTENSITY=.20 E(r)=.01 COV = 0 CV=.25
INTENSITY=.50 E(r)=.01 COV = 0 CV=.25
INTENSITY=.05 E(r)=.01 COV < 0 CV=.25
INTENSITY=.10 E(r)=.01 COV < 0 CV=.25
INTENSITY=.20 E(r)=.01 COV < 0 CV=.25
INTENSITY=.50 E(r)=.01 COV < 0 CV=.25
MEDIAN EXTINCTION TIME
LOG DISTURBANCE FREQUENCY
-3.00
-2.00
-1.00
0.00

D


INTENSITY=.05 E(r)=.1 COV > 0 CV=.25
INTENSITY=.10 E(r)=.1 COV > 0 CV=.25
INTENSITY=.20 E(r)=.1 COV > 0 CV=.25
INTENSITY=.50 E(r)=.1 COV > 0 CV=.25
INTENSITY=.05 E(r)=.1 COV = 0 CV=.25
INTENSITY=.10 E(r)=.1 COV = 0 CV=.25
INTENSITY=.20 E(r)=.1 COV = 0 CV=.25
INTENSITY=.50 E(r)=.1 COV = 0 CV=.25
INTENSITY=.05 E(r)=.1 COV < 0 CV=.25
INTENSITY=.10 E(r)=.1 COV < 0 CV=.25
INTENSITY=.20 E(r)=.1 COV < 0 CV=.25
INTENSITY=.50 E(r)=.1 COV < 0 CV=.25
MEDIAN EXTINCTION TIME
LOG DISTURBANCE FREQUENCY



$$\underline{A} = \begin{bmatrix} (1-C_2)(1-C3) & \pi_d & \cdots & \pi_d & \pi_d \\ (1-C_1)C_2 & 1-\pi_d & & 0 & (1-\pi_d)\pi_c \\ C_1(1-C_2) & 0 & (1-C_2)(1-\pi_d) & & 0 \\ C_1C_2 & 0 & C_2(1-\pi_d) & (1-\pi_d)(1-\pi_c) & \end{bmatrix}$$

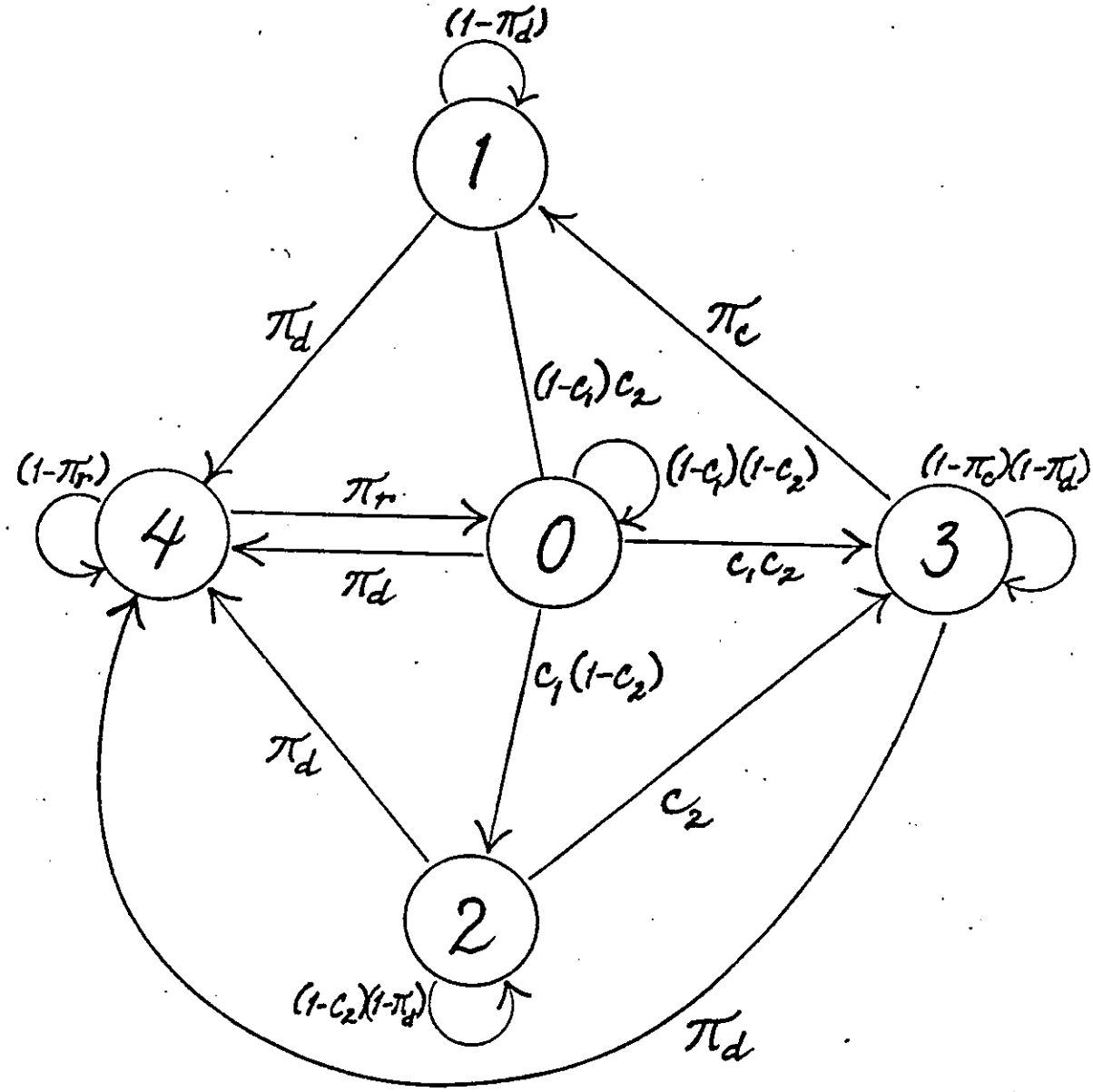
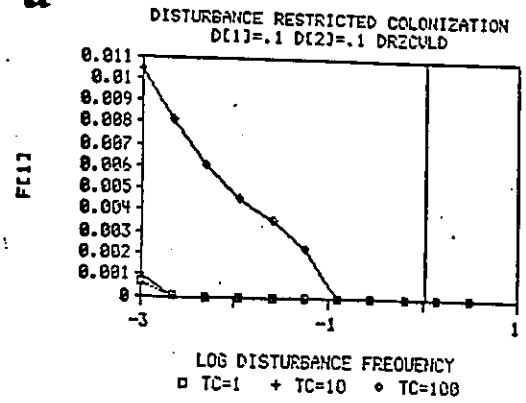
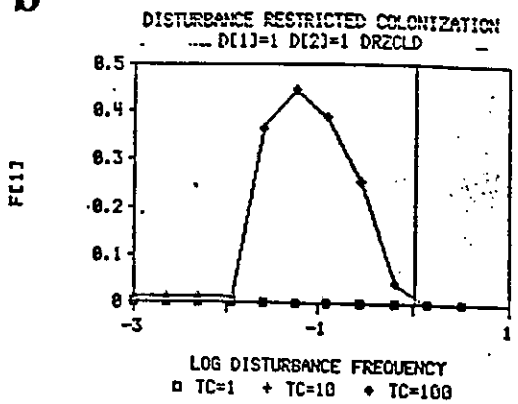

$(1-\pi_d)$
1
π_d
$(1-c_1)c_2$
π_c
$(1-\pi_r)$
4
π_r
0
$(1-c_1)(1-c_2)$
$(1-\pi_c)(1-\pi_d)$
3
π_d
c_1c_2
$c_1(1-c_2)$
π_d
c_2
2
$(1-c_2)(1-\pi_d)$
π_d

Fig 1

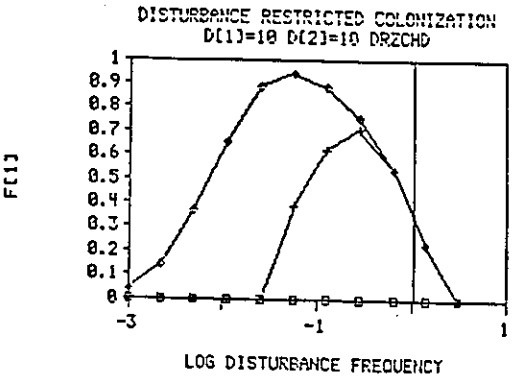
a


DISTURBANCE RESTRICTED COLONIZATION
D[1]=.1 D[2]=.1 DRZCULD
F[1]
0.011
0.01
0.009
0.008
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

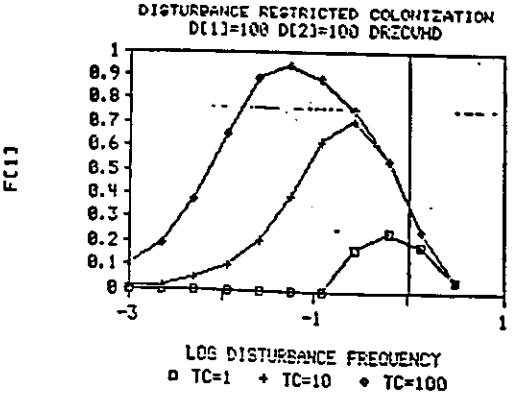
b


DISTURBANCE RESTRICTED COLONIZATION
D[1]=1 D[2]=1 DRZCLD
F[1]
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

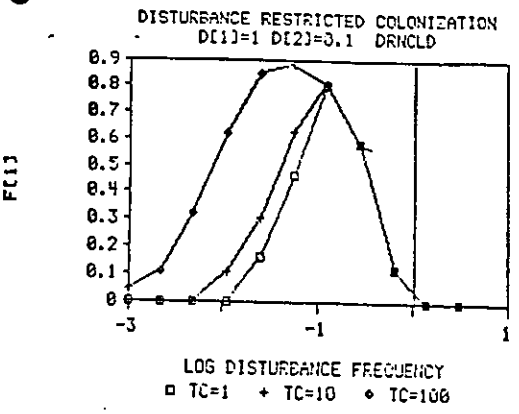
c


DISTURBANCE RESTRICTED COLONIZATION
D[1]=10 D[2]=10 DRZCHD
F[1]
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY

d


DISTURBANCE RESTRICTED COLONIZATION
D[1]=100 D[2]=100 DRZCVHD
F[1]
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

e


DISTURBANCE RESTRICTED COLONIZATION
D[1]=1 D[2]=0.1 DRNCLD
F[1]
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

f

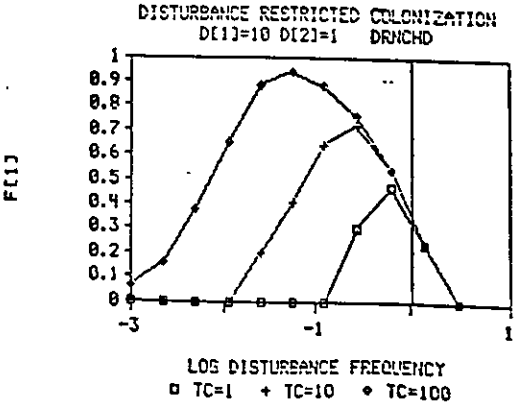
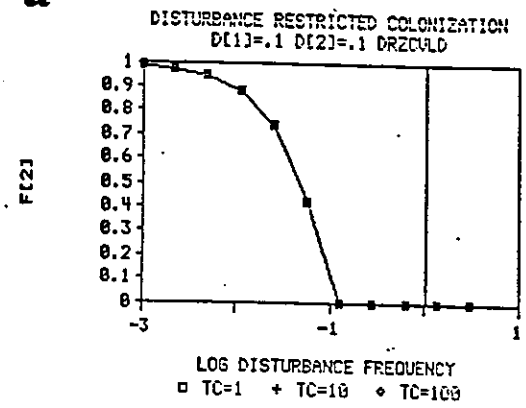

DISTURBANCE RESTRICTED COLONIZATION
D[1]=10 D[2]=1 DRNCHD
F[1]
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

Fig 2

a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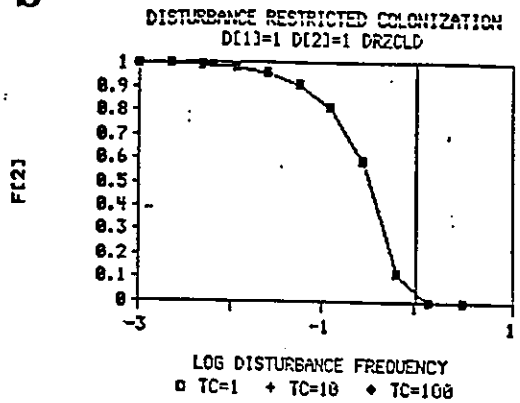
b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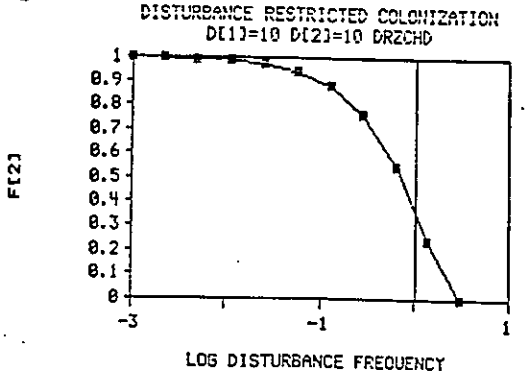
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F[2]
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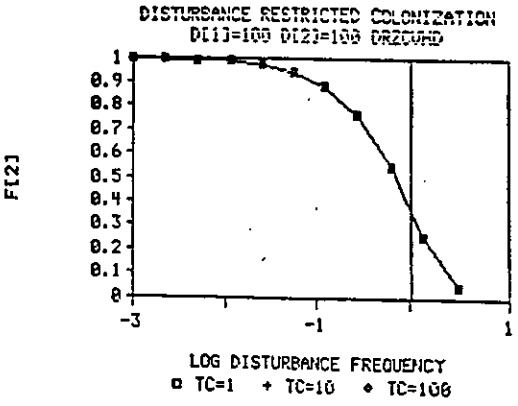
d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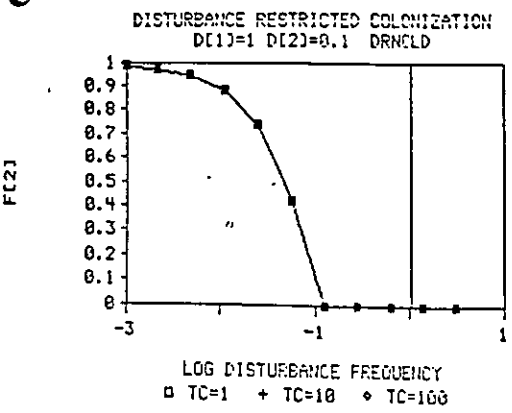
e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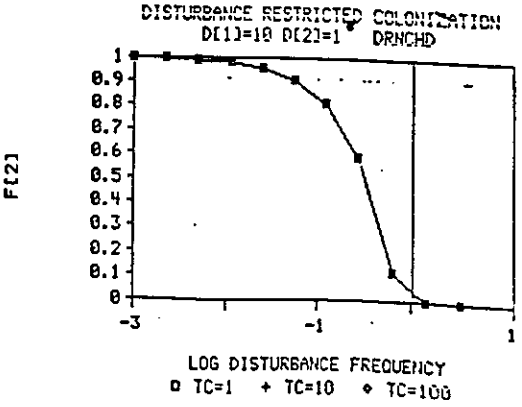
f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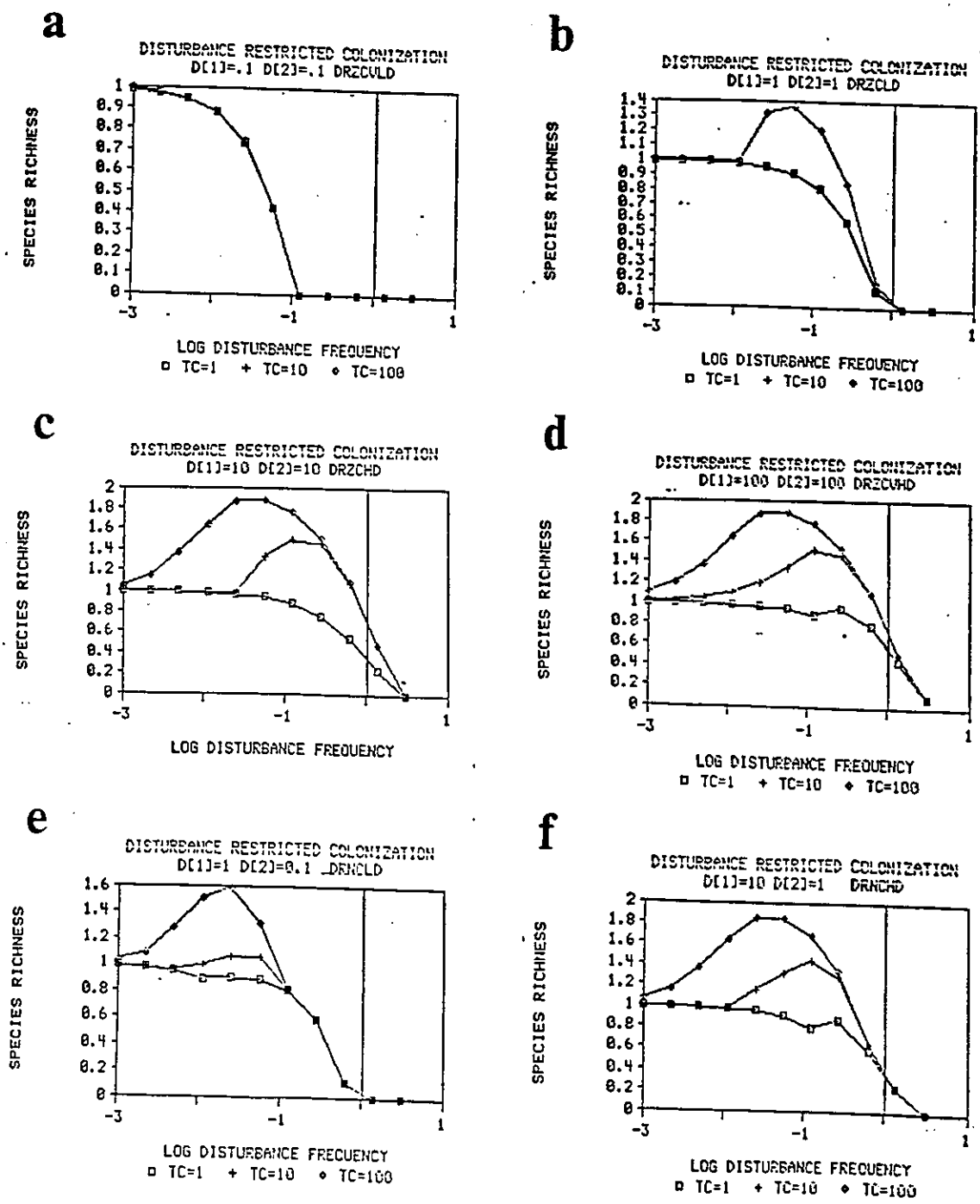
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SPECIES RICHNESS
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100
c
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SPECIES RICHNESS
LOG DISTURBANCE FREQUENCY
d
DISTURBANCE RESTRICTED COLONIZATION
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SPECIES RICHNESS
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100
e
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LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100
f
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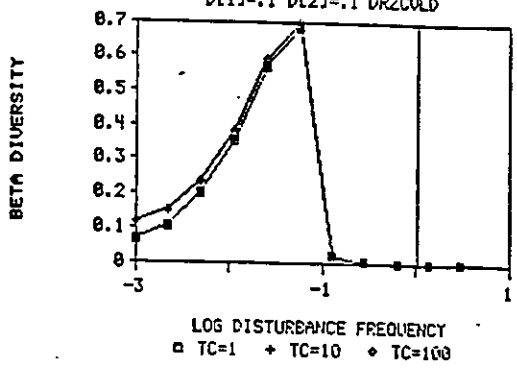
LOG DISTURBANCE FREQUENCY
TC=1 + TC=10 ◆ TC=100

a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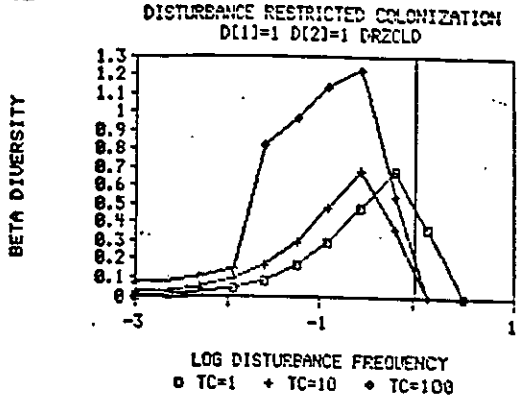
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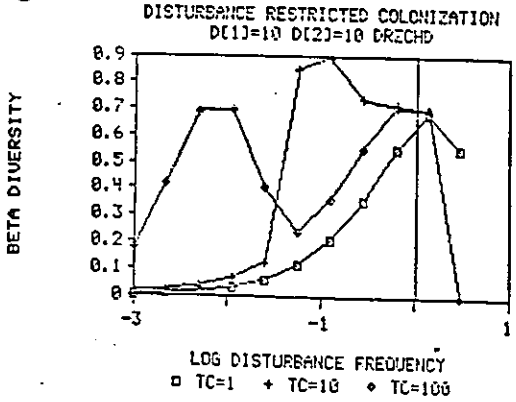
c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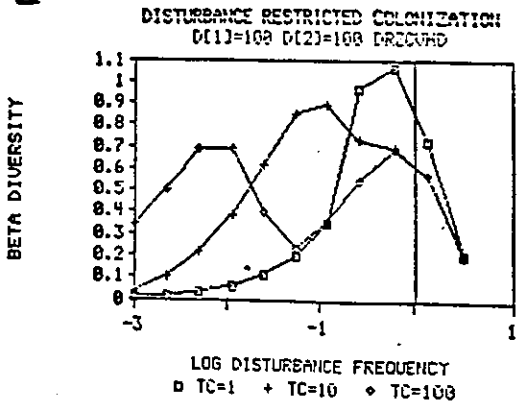
d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LOG DISTURBANCE FREQUENCY
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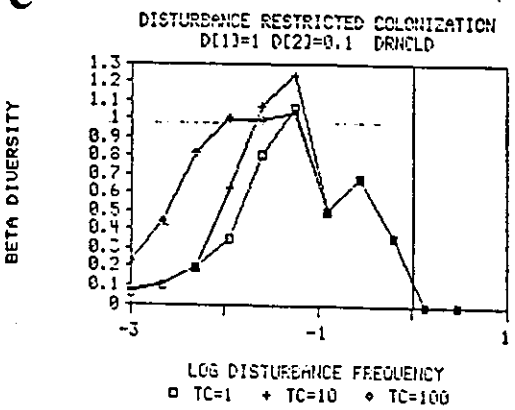
e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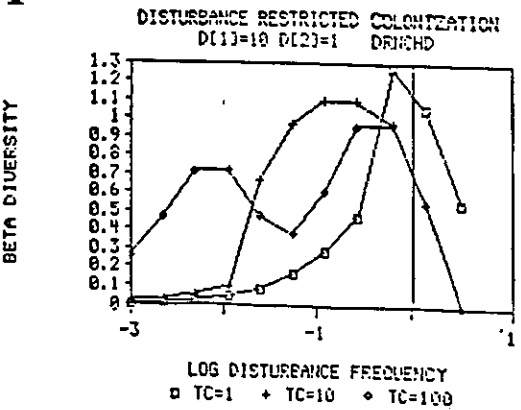
f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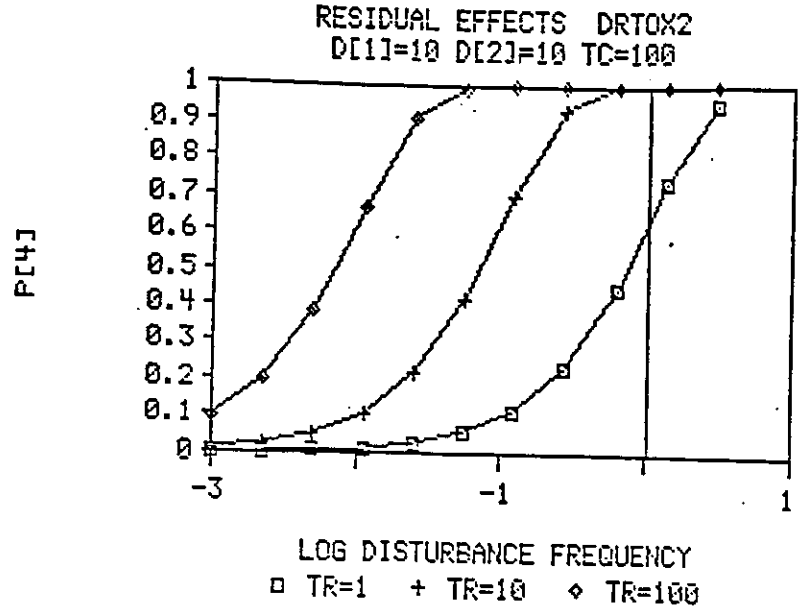
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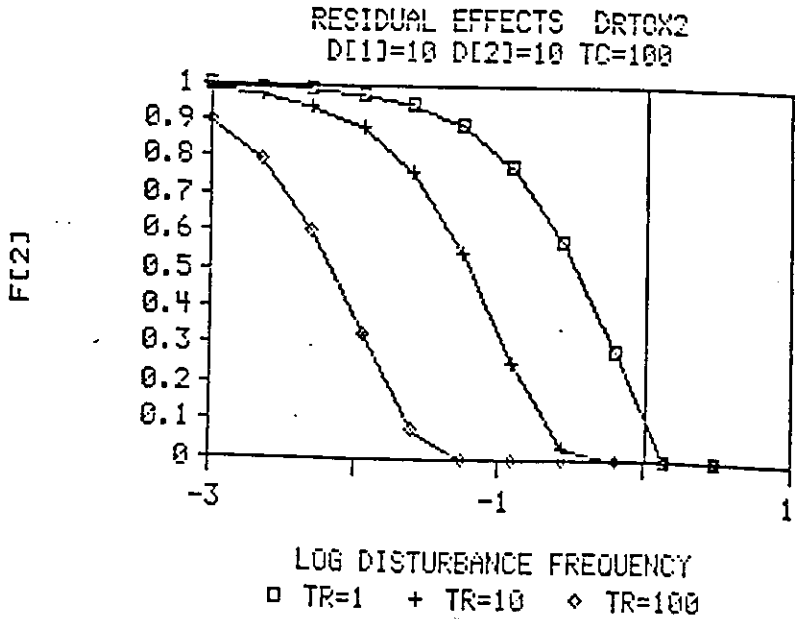
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TR=1
TR=10
TR=100

b


RESIDUAL EFFECTS DRTOX2
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F[2]
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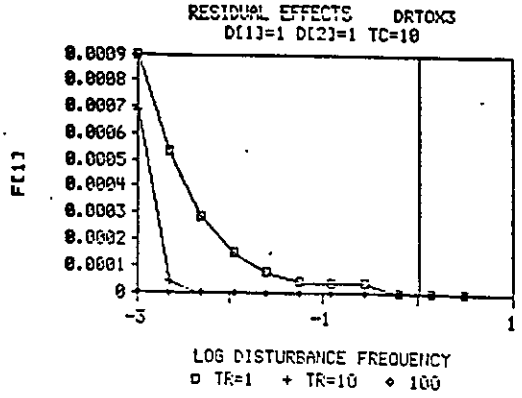
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TR=1
TR=10
TR=100

a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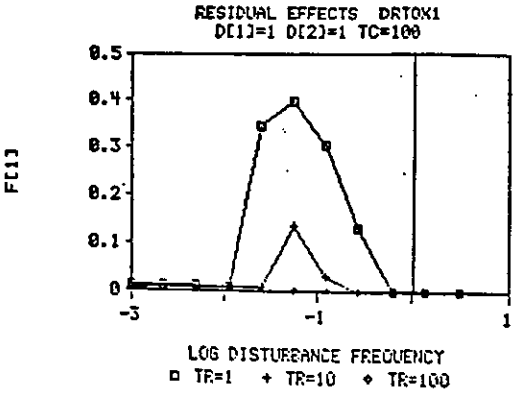
0.0007
0.0006
0.0005
0.0004
0.0003
0.0002
0.0001
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ 100

b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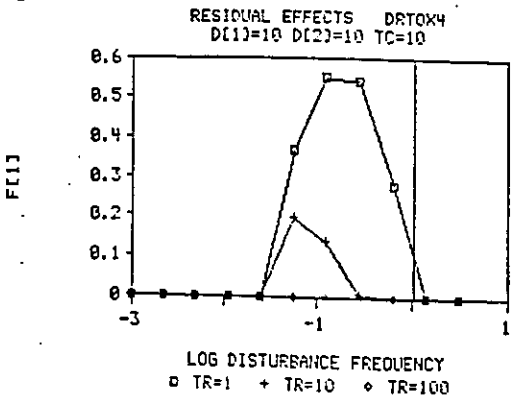
0
-3
-1
1
LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ TR=100

c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0
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-1
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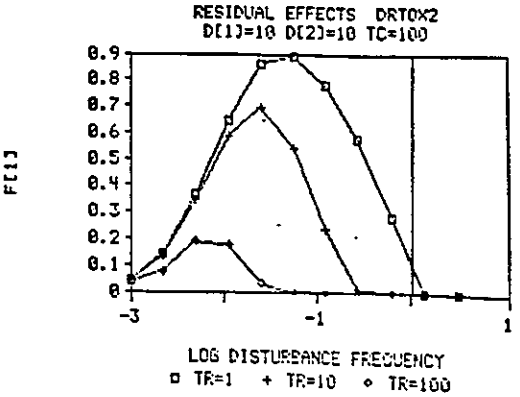
LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ TR=100

d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0.5
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LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ TR=100

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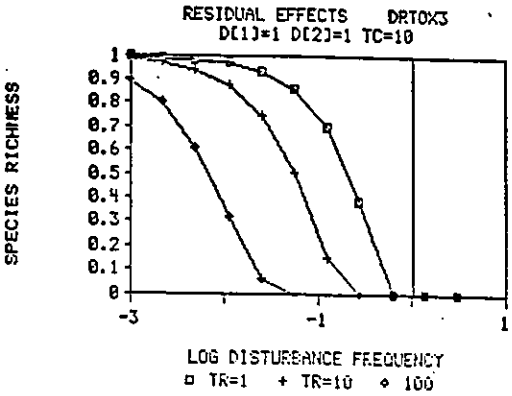
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LOG DISTURBANCE FREQUENCY
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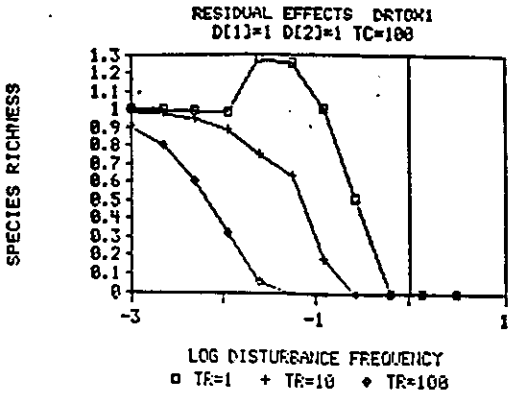
b


RESIDUAL EFFECTS DRTOX1
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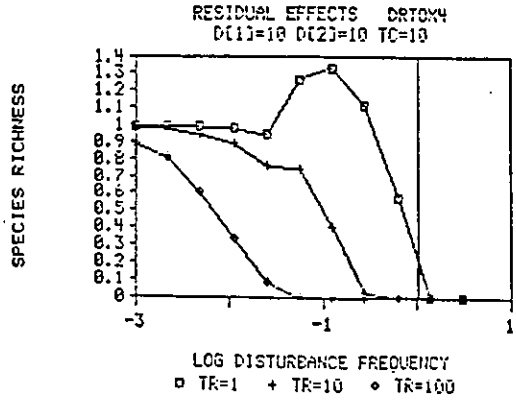
SPECIES RICHNESS
LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ TR=100

c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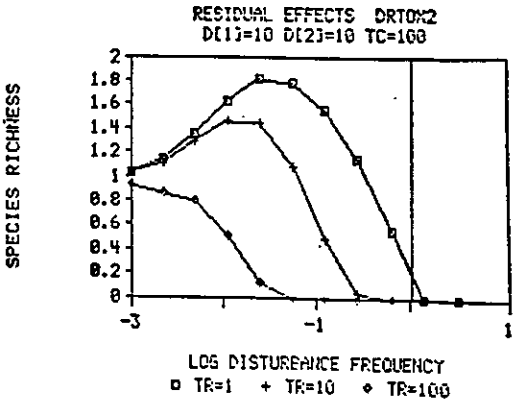
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LOG DISTURBANCE FREQUENCY
TR=1 + TR=10 ◇ TR=100

III. Body Burdens of Contaminants

John W. Farrington, Bruce W. Tripp and Alan C. Davis

Introduction

This section of the report reviews available data on budy burdens of organic chemicals and trace metals of environmental concern. Although the specific task is to assess body burdens for deep ocean organisms living below 1000 meters with an emphasis on benthos, the paucity of such data forced us to consider other open ocean biota and higher predators such as marine mammals in order to have a basis for discussion of what might be expected from future studies and to discern what knowledge can be transferred from studies of coastal/continental shelf areas to the deep sea communities.

The paucity of data for deep sea organisms also led us to undertake analyses of a set of deep sea fish in collaboration with Dr. John Stegeman to provide state-of-the-art analyses of organochlorine compound body burdens.

This section contains five subsections:

III. 1. Organic Chemical Contaminants

- review of pertinent data

III. 2. New Body Burden Data

- results of organochlorine analyses obtained for this project

III. 3. Metal Body Burdens

- review of pertinent data

III. 4. Existing Coastal/Continental Shelf Knowledge

- discussion of existing data on body burdens and how it applies to the deep sea. Recommendations of how to extrapolate from the present data and knowledge

III. 5. Summary and Recommendations

III. 6. Bibliography

- description of search process and bibliographic listings

We gratefully acknowledge the assistance of the W.H.O.I. Librarian's staff in compiling the bibliography. Dr. Nelson M. Frew and Mr. Carl Johnson of the W.H.O.I. GC/MS facility provided superb GC/MS analyses via the application of sophisticated pulsed positive ion negative chemical ionization (PPINICI) GC/MS analyses for the samples. Ms. Peggy Chandler typed this section of the report in record time.

III. 1. Organic Chemical Contaminants

The data for body burdens of organic chemical contaminants in deep ocean (below 1000 meters) organisms are meagre and are mainly for chlorinated pesticides and polychlorinated biphenyls (PCBs). We have included data in upper ocean organisms, because they may be relevant to transfer of contaminants to the deep ocean. We have also included some data on large predatory fish and marine mammals as these data may give clues as to the contaminants that are transferred back to man.

Organochlorines

Before reviewing the available data it is important to briefly discuss changes in methodology for analyses of organic compounds in environmental samples over the period of 1970 to the present. The example of the organochlorine compounds will be used although similar progress has been made for fossil fuel hydrocarbons.

Figure 3.1.1 presents structures of several of the organochlorine pesticides and PCBs for reference. Historically, the DDT family compounds and other chlorinated pesticides such as dieldrin were analyzed by packed column gas chromatography (GC) with detection by a detector sensitive to halogen atoms (e.g. an electron capture detector). It was discovered that PCBs interfered with the analysis of DDT family compound and, as resolution of packed column gas chromatography improved, the chromatograms were examined in more detail. Typical chromatograms of the period, taken from Harvey et al. (1974) are presented in Figure 3.1.2. As the resolution and sensitivity of gas chromatography progressed it also became apparent that the mixture of polychlorocam-

phenes constituting the pesticide Toxaphene(R) are interfering with some of the analyses of PCBs (e.g. Ballschmiter et al., 1981; Ribick et al., 1982; Musial and Uthe, 1983).

Figure 3.1.3 presents medium to high resolution glass capillary gas chromatograms (GCGC) of a standard mixture of several pesticides, Aroclor 1254 mixture of PCBs and Toxaphene. All of these compounds represented by individual peaks in the capillary gas chromatograms may be mixed in an environmental sample and the correct interpretation of the poorly resolved packed column gas chromatograms is obviously very difficult. Some clean-up techniques to separate some of these compounds by column chromatography prior to packed column gas chromatography have been used, however, the data for xenobiotic organochlorine compounds in open ocean ecosystems, as meagre as it is, suffers from another constraint. From 1970 to the present, data for DDT family compounds, other chlorinated pesticides and PCBs was produced during a time of transition from the packed column GC to the present situation of higher resolution analyses. In most cases there is no reasonable way to strictly compare older data from the packed column analyses of the early to mid-1970's with the newer, higher resolution data produced since the late 1970's. Few laboratories have made an effort to compare data obtained by both methods on the same samples. Risebrough and co-workers have shown reasonably good agreement between packed column GC and glass capillary GC measurements for PCBs in mussel tissue (Galloway et al., 1984). However, it is risky to extrapolate such data to other tissues where metabolism or other factors may have caused compositional changes in the PCBs.

Even with high resolution GCGC analyses, intercomparison exercises among several laboratories show that some laboratories still have problems with in-

dividual compound analyses at precisions or accuracies required for certain types of environmental monitoring programs (Uthe and Musial, 1981).

These constraints must be kept in mind in the following discussions of data from various sources. A lack of intercomparison data of state-of-the-art analyses and a lack of data quality control as defined by the NOAA Data Quality Assurance program mandate that comparisons of data from different laboratories be made with extreme caution. Ocean dumping monitoring programs to detect spatial and temporal trends will require stricter interlaboratory comparisons and quality control than have been used to date.

Harvey and Steinhauer (1976) report on DDT family compounds and PCBs in benthic animals from the Nares Abyssal Plain (Table 3.1.1). These data clearly indicate penetration of PCBs and DDT to the deep ocean in forms available for biological uptake. Barber and Warlen (1979) summarize a few earlier data from their laboratory as well as several additional analyses for DDT family compounds in livers of rattails, Antimora rostrata collected during 1972, 1973, 1974 from the continental slope off North America (Table 3.1.2). Risebrough et al. (1976) report on PCBs in two of these same fish livers (Table 3.1.3). Organochlorine concentrations in all of the preceding data were obtained by packed column gas chromatography.

Barber and Warlen (1979) point out that the concentrations of organochlorine residues in the A. rostrata and other deep sea fish measured up to that time were similar to concentrations measured in livers of cod taken from the Atlantic coast by Sims et al. (1977). In discussing Sims' et al. (1977) data, Barber and Warlen note those authors reported an increase in organochlorine concentrations for fish caught near population centers in comparison

to those from more remote areas. Barber and Warlen then state "It would be possible to collect Antimora rostrata from 2500 meters at various sites along the continental margin of the east coast of North America to determine whether or not population centers such as New York were affecting the concentration of residues in the fish on the adjacent deep sea." They predicted that horizontal dispersion by currents would prevent any elevations of residues associated with population centers but this hypothesis has yet to be tested.

Krämer et al. (1984) summarize the elegantly detailed analytical chemistry of Ballschmiter and coworkers at the Universität Ulm, Federal Republic of Germany on the application of high resolution GCGC analyses of C_6-C_{14} organochlorine compounds in selected biota from around the world (Zell et al., 1980a,b; Ballschmiter et al., 1981). These analyses include several cod livers and tissues from other upper ocean and nearshore fish as well as a specimen of Aphanos carbo (black scabbard fish) caught near Madeira at depths of 800-1200 meters. They report concentrations of hexachlorobenzene, several chlorobiphenyls, many of the DDT family of compounds, heptachlor, cis-chlordane, trans-chlordane, trans-Nonachlor, Mirex, oxychlordane, dieldrin, endrin, and Toxaphene$^{(R)}$ (Table 3.1.4).

We will discuss the implications of this data further when we present our own data on organochlorines in livers of rattails obtained as part of the work on this project (Section III-2).

There are numerous references to the organochlorine compounds in marine mammals (Wolmann and Wilson, 1970; Addison et al., 1972; Taruski et al., 1975; Tanabe et al., 1981, 1983; Gaskin et al., 1971; Gaskin et al., 1974; Henry and Best, 1983; Aguilar, 1983; Knap and Jickells, 1983). Many references concerning coastal marine mammals were intentionally not collected for this report.

Blubber from 18 cetaceans including humpback, sperm, densebeaked, Atlantic and Pacific pilot whales and five species of dolphin were analyzed for DDT, PCBs, chlordane and dieldrin by Taruski et al. (1975). These authors also summarized data on organochlorines in cetaceans up to that time. All except two of their own samples were taken off the east coast of North America (Table 3.1.5). The authors note that tissue concentrations are sufficiently elevated to cause serious concern about possible reproductive effects if they extrapolate from effects noted in other mammals.

Knap and Jickells (1983) reported data from samples of four goosebeaked whales (Ziphius cavirostris), a toothed species distributed worldwide in deeper waters and reportedly feeding mainly on squid and deep water fish. Their samples were from Bermuda and concentrations of DDT and PCB were within the range reported by Taruski et al. (1975) (Table 3.1.5). Henry and Best (1983) analyzed blubber of 29 minke, 6 fin, and 1 sei whale landed at the Durban whaling station of the Republic of South Africa in 1974. It is significant that these authors noted that DDT family compounds were much lower on the average than for similar baleen whales from the North Atlantic but were in the same range as concentrations measured in comparable species from the Antarctic and the North Pacific. For 12 sperm whales landed in in Durban 1974 DDT family compounds were much lower in concentration than for sperm whales from any other locality examined up to that time; but the relative youth of the samples might be a reason for this. A most significant finding was that no PCBs were detected at the 0.5×10^{-6} g/g wet weight level of detection. These authors summarize data for organochlorines in whales published by other authors.

Fourteen sperm whales (Physter macrocephalus) caught off Spain's northwest coast were analyzed for DDE, DDT, DDD, and PCB by Aguilar (1983). He noted

that organochlorine residue levels of sperm whales seem to be in an intermediate position with regard to other cetaceans in the same general area and he further suggested this might be due to their feeding deeper in the water column on a variety of prey. Tanabe et al. (1983) review their large data set for PCBs, DDTs, and HCHs in marine mammals and conclude that the concentration ratio of DDT to PCB is greater in the southern hemisphere because PCBs are, or were, predominantly released to the environment in the northern hemisphere. Also, DDT use in the tropics and southern hemisphere has continued over the past decade while use in the northern hemisphere has been reduced. The link between use of and release of compounds to the environment and occurrence in marine mammals or sea turtles results from poorly understood complicated biogeochemical cycles of xenobiotic compounds in the environment. This link will be briefly discussed later in this report. Part of the transfer process can involve food chain or food webs.

There are limited data about body burdens of organochlorines in pelagic and mesopelagic organisms of the open ocean. Data for the Atlantic Ocean results almost exclusively from the pioneering efforts of Harvey et al. (1974), Risebrough and coworkers (summarized in Risebrough et al. (1976)) and Giam et al., 1976, 1978). This is exemplified by the data of Harvey and colleagues presented in Tables 3.1.1, 3.1.6, 3.1.7, and 3.1.8. All these data are based on packed column gas chromatographic analyses and used analytical methods subjected to international intercomparison exercises. Thus, they were among the best possible at that time. Figure 3.1.4 summarizes that data.

Harvey et al. (1974) offer some general conclusions:

i) There is little evidence of food web magnification. Higher level predators (except marine mammals) show inconsistent trends. Sharks showed high

burdens of PCBs and DDT while barracuda have reduced concentrations by two orders of magnitude according to the combined intercalibrated data of Harvey et al. (1974) and Giam et al. (1972). The lack of food web magnification was explained by the different lipid levels and lipid types in various organisms and by exchange with the water across membrane surfaces such as gills as discussed by Hamelink et al. (1971).

ii) PCB/DDT ratios showed some intriguing differences for the various components of the oceanic food webs. The exact reasons for this was not apparent at that time.

Giam and coworkers report data for organochlorine in plankton (Giam et al., 1973); crustacea and fish (Giam et al., 1972, 1978) from the Gulf of Mexico and Northern Caribbean. These samples were primarily surface water or nearshore biota. Baird et al. (1975) sampled 1052 mesopelagic fishes and zooplankton at 5 stations in the Gulf of Mexico. They analyzed 29 pooled samples for DDT and PCBs and report this data (Table 3.2.9) and several interesting hypotheses/ conclusions. Baird et al. report:

i) Surface zooplankton contain higher concentrations than those living deeper in the water column.

ii) Tentative evidence indicates that organochlorines accumulate at higher trophic levels based on zooplankton/fish ratios. However, the authors noted that the equilibria with surrounding water hypothesis of Hamelink et al. (1971) might contribute to the observed concentrations.

iii) Deep living species (330-380 meters) which spend most of their lives below sources of primary production had concentrations of chlorinated hydrocarbons comparable to species undergoing diel vertical migration.

iv) In some cases, significant concentration differences were seen in the same species taken at the same depth and at different depths.

v) Specimens of the same species but of different sizes had order of magnitude differences in concentrations.

vi) Concentrations of PCBs were one to two orders of magnitude higher for Gulf of Mexico organisms compared to the oceanic Atlantic species analyzed by Harvey et al. (1974). Gulf of Mexico organisms were at least as high as mesopelagic fishes of the Gulf of California (MacGregor, 1974).

Bernhard (1978) summarized data for organochlorine contaminant compounds for the Mediterranean Sea up to that date. His compilation contained data for mainly nearshore and upper ocean species. Fowler and Elder (1980-1981) analyzed pelagic organisms from the open Mediterranean Sea for PCBs and DDT. Although they correctly cautioned the limited number of samples analyzed, they noted:

i) total DDT/PCB ratio was significantly higher in euphausiids from the central region compared to the eastern sector and hypothesized this was due to greater use of DDT in the northeastern Mediterranean;

ii) although no trends of increasing concentrations with increasing size of myctophids, the ratio of ΣDDT/PCBs changed, perhaps indicating different rates of metabolism of these two groups of compounds;

iii) no evidence for food chain or trophic level magnification was noted, a hypothesis tested by analyses of a well characterized food web of several trophic levels at one station (Fowler and Elder, 1978). The authors presented a nice summary table of PCBs in mixed plankton samples as reported by several authors (Table 3.1.10). They conclude "On the assumption that our analytical

techniques are intercomparable with those used in the other surveys, we can conclude that at present average PCB levels in many open Mediterranean biota are similar to or, in some cases, slighly lower than those reported in similar species from different geographical areas."

Stout (1979) reported organochlorines (dieldrin, endrin, DDT, PCBs) in surface water and commercially important continental shelf fish species from the northwest Atlantic Ocean and Gulf of Mexico. Species with higher lipid content more consistently contained detectable concentrations. Significant correlations were found between lipid content, size and concentrations of PCBs and total DDT for some species.

Sims et al. (1977) analyzed 261 samples representing 29 species of crustacea, bivalves and finfish from the nearshore and continental shelf waters of the Canadian Atlantic coast. Only fatty specimens of pelagic finfish consistently contained more than 0.1×10^{-6} g/g of PCB and DDT. No significant differences were found in the concentrations between the locations sampled. Freeman et al. (1984) report data for PCBs, organochlorine pesticides and chlorobenzenes in livers of 100 Atlantic cod (Gadus morhua) caught over an 8-year period off Halifax, Nova Scotia, Canada. These authors state that over the eight years ending in 1980 PCBs and DDT showed a general decline between 1972 and 1975 with no significant change after 1975. Concentrations of other organochlorines did not change between 1972 and 1980. Falandysz (1981) reported data for cod liver oil from a factory in Gdynia, Poland processing cod of Baltic Sea origin. Samples were monitored for HCB, PCBs and DDT between 1971 and 1980. However, in some years only one sample was analyzed. DDT seemed to decline by a factor of 2 to 3 while HCB and PCBs showed no decline.

Fossil Fuel Hydrocarbons and other Organic Contaminants

The data for body burdens of fossil fuel hydrocarbons from petroleum or from fossil fuel combustion inputs is derived almost exclusively from the analysis of coastal and continental shelf biota. Those data are extensive and complicated and a general state-of-the-knowledge synopsis is sufficient for purposes of this report. They will be discussed in Section III. 4. The small amount of data available for hydrocarbons in open ocean organisms is discussed here.

Shehekaturina and Mironov (1979) report on hydrocarbons in a few species of pelagic and bottom fish from the Mediterranean. However, the depth and location of capture (other than Western Mediterranean) were not specified. Also, their analyses by low resolution packed column gas chromatography could detect only very high concentrations of petroleum and these concentrations were not found. Similar data using similar analytical techniques were presented for a more numerous collection of organisms from the Mediterranean Sea, Atlantic Ocean, Indian Ocean and Black Sea. Again locations and depths of sampling were not specified (Mironov et al., 1981).

Burns and Teal (1973) and Butler et al. (1983) report data on estimates of petroleum hydrocarbons in the pelagic Sargassum community of the Sargasso Sea. Concentrations ranging between non-detectable and $1{,}764 \times 10^{-6}$ g/g dry weight were found. There is little doubt that petroleum contamination, presumably from tar residues and tanker washings contaminate this pelagic community. Of interest to this discussion is the report, accompanied by a photograph, of a small tar particle in a fecal pellet of Litiopa melanostoma (snail) (Butler et al., 1983). This is dramatic evidence of one transport mechanism that can

move hydrocarbons to the ocean depths. The authors also noted no evidence of food web magnification among the pelagic biota, a finding similar to that report for organochlorines as discussed above. This data is summarized in Tables 3.1.10 and 3.1.11 from Butler et al. (1983) and Table 3.1.12 from Burns and Teal (1973).

Teal (1976) reports a few data for hydrocarbons in benthos of the Nares Abyssal Plain which indicate levels of petroleum hydrocarbon contamination within the range found for the pelagic Sargassum community.

Giam et al. (1978) have reported on phthalate esters present in biota of the pelagic and nearshore community of the Gulf of Mexico. Concentrations of diethylhexyl phthalate (DEHP) range from non-detectable ($< 1.0 \times 10^{-9}$) to 135×10^{-9} g/g wet weight. These authors noted that DEHP production was substantially more than PCB production yet DEHP concentrations were much lower than PCB concentrations. They conclude that substantial microbial degradation of DEHP in the environment or substantial metabolism of DEHP in the biota relative to PCB metabolism must occur.

A very special case of organic chemical contamination of the continental slope off the U.S. Atlantic Coast occurred near 39°38'N, 71°02'W during 1967-1968. Surplus World War II ships were scuttled with obsolete chemical warfare munitions; mustard gas, nerve agent VX, nerve agent GB, (Sarin) and CS riot control reagent. Surveys conducted in 1969 and 1972 located some of the ships on the bottom and analyses of water and sediment samples taken nearby did not detect any of the disposed materials at that time (Wilkness, 1973). Agent GB would hydrolyze relatively rapidly in the slightly alkaline seawater conditions, while Agent VX would require a longer, undetermined time for hydrolysis.

Most of the analytical methods employed by Wilkness were adapted from analytical techniques used to detect these materials in fresh water systems. Details of methodology were not presented, thus it is difficult to evaluate this data further. There were no analyses of biota samples to detect the presence or confirm the absence of the chemical warfare agents.

Unpublished information suggests there may be other such disposal sites on the continental slope or rise off the U.S. east and west coast. These sites could be used as experimental study sites to assess the potential impact of ocean dumping of certain chemicals. Such work would obviously require consultation between DOD and NOAA. The analyses conducted to date (Wilkness, 1973) were appropriate surveys and an admirable accomplishment given the state-of-the-art at that time, but they are inadequate to meet most criteria currently applied to ocean dumping environmental assessment/environmental impact studies.

Summary

Few data exist for body burdens of organic contaminants in biota of the deep ocean. Most of the available data are for North Atlantic deep water organisms. Whenever analyses have been conducted, detectable concentrations of some chlorinated pesticides, PCBs and petroleum hydrocarbons have been found. This is consistent with what is known of oceanic biogeochemical cycles as will be discussed in Section III. 4.

The available data indicates that food web transfer of organic pollutants can occur, but food web magnification is not the rule. Rather, exposure levels, size, age, feeding habitat, lipid content, ability to metabolize xenobiotic compounds (see Section IV), and ability to exchange compounds to the water across membrane surfaces are the controlling factors for body burdens.

The relative importance of each of these factors is poorly understood. Marine mammals (and birds) may be exceptions and may exhibit food web magnification because of an inability to exchange compounds with water directly across gill surfaces. However, age, size, lipid content and the factors other than food web magnification may be dominant in these cases as well.

The interpretation of the collected data is severely hampered by progressively changing analytical methodology for analyses of organic chemical contaminants and by the lack of adequate quality assurance and intercomparison exercises for many of the laboratories reporting data. For example, such seemingly minor issues as determination of lipid content of biota and subsequent reporting and comparison of organochlorine compounds on the basis of normalization to lipids is fraught with error. Standardized or comparable lipid determinations are the exception rather than the rule.

It has been known for over a decade that pollutant chemicals mobilized by man and released to land, nearshore areas, and the atmosphere can penetrate to the deep ocean in the time span of a decade or less. The body burden data, limited though they are, clearly indicate that a portion of these organic chemical pollutants are biologically available. The biogeochemical cycles that might be involved are briefly discussed in Section III. 4.

Table 3.1.1 (from Harvey and Steinhauer, 1976 - Table 15.1)
PCB and t-DDT in Deep Atlantic Benthos[a]

Specimen	DDT	DDE	PCB	PCB/t-DDT
	(in parts per billion wet weight)			
Rattail Stomach	b	0.6	0.0	
Rattail Fillet	b	21.4	0.5	0.02
Rattail Liver	b	381.0	340.0	0.9
Brotulid Stomach	0.5	4.4	11.5	2.3
Brotulid Fillet	1.7	2.2	36	9
Brotulid Liver	56	1800	1200	0.6
Holothurian #1 Stomach	b	0.2	0.2	1.0
Holothurian #1 Body	b	0.2	0.0	0.0
Holothurian #2 Stomach	1.1	0.2	0.6	0.46
Holothurian #2 Body	0	0.1	0.5	1.0
Core A-II-85-3-6 (0-2 cm)[a]	b	0.5	0.3	0.6

[a]Collected near 25°N, 62°W in 5500-5800 m water depth on Atlantis II cruise 85 (September, 1974).

[b]Saponified before analysis.

Table 3.1.2 (from Barber and Warlen, 1979)
Organochlorine insecticide residues in mg/wet kg in Antimora rostrata livers.
Fish were collected from 2500 m at 34°18.2'N, 75°32.6'W.

Specimen No.	p,p'-DDE	p,p'-DDD	p,p'-DDT	o,p'-DDT	ΣDDT	dieldrin
			1972			
30	1.98	0.77	4.54	0.24	7.53	0.03
31	0.69	0.35	1.76	0.13	2.93	0.02
32	1.56	0.67	2.81	0.29	5.33	0.01
33	1.58	0.69	3.48	0.18	5.93	0.01
X	1.45	0.62	3.15	0.21	5.43	0.02
s	0.54	0.19	1.17	0.07	1.91	0.01
			1973			
404	1.14	0.35	1.46	0.12	3.07	0.01
405	0.55	0.21	0.79	0.07	1.62	0.01
407	3.28	0.65	2.61	0.20	6.74	0.03
X	1.66	0.40	1.62	0.13	3.81	0.02
s	1.44	0.22	0.92	0.07	2.63	0.01
			1974			
400	0.58	0.27	1.34	0.13	2.32	0.01
402	2.53	0.72	2.70	0.21	6.16	0.03
403	12.45	2.48	11.58	0.80	27.31	0.01
X	5.19	1.16	5.21	0.38	11.93	0.02
s	6.37	1.17	5.56	0.37	13.46	0.01

Table 3.1.3 (from Risebrough et al., 1976)

Organochlorines in Antimora rostrata liver, reported as

10^{-6} g/g lipid

Specimen No.	p,p'-DDE	p,p'-DDT	o,p'-DDT	p,p'-DDD	ΣDDT	PCB
1	5.9	2.4	0.6	2.4	11.3	3.8
2	19	12	3.1	5.2	39.3	12.5

Table 3.1.4 (from Krämer et al., 1984)

Organochlorine pollutants in a deep sea fish of the eastern North Atlantic near Madeira. All values in microgram/kilogram (ppb)

	Marine Water Deep Sea Black Scabbard Fish (Liver)
HCH (BHC)	
α-HCH	< 0.1
β-HCH	< 0.1
γ-HCH	< 0.1
Δ-HCH	< 0.1
HCB	17
PCB	
28	45
52	105
101	305
138	930
153	570
180	410
ΣPCB (60 % Cl)	5800
DDT	
4,4'-DDT	5060
4,4'-DDD	1100
4,4'-DDE	3030
4,4'-DDMU	d.*
4,4'-DBP	d.*
ΣDDT**	9190
2,4'-DDT	390
2,4'-DDD	< 0.1
2,4'-DDE	< 0.1
Cyclodiene - Pesticides	
Heptachlor	< 0.1
cis-Chlordane	250
trans-Chlordane	80
trans-Nonachlor	245
Mirex	32
Oxychlordane	20
Dieldrin	35
Endrin	< 0.1
Polychloroterpenes***	
Toxaphene	50-1000

*0.1 < d < 1

**ΣDDT = 4,4'-DDT + 4,4'-DDD + 4,4'-DDE + 4,4'-DDMU

***not quantified, present in the 50 - 1000 µg/kg (lipid basis) range;
HCH = Hexachlorocyclohexane; BHC = Benzenehexachloride = HCH;
HCB = Hexachlorobenzene; PCB = Polychlorobenzene
DDMU = 2,2-Dio(4-chlorophenyl-1-chloroethene
DBP = Dichlorobenzophenone

Table 3.1.5 (from Taruski et al., 1975)
Concentration of organochlorine residues in blubber of cetaceans, in parts per million (ppm), wet weight; ND, not detected. PCB is reported as Aroclor 1254 except for samples 8, 9, and 15, which are reported as Aroclor 1260.

Sample No.	Species	Sex status	Location	PCB (ppm)	Σ-chlordane (ppm)	Dieldrin (ppm)	DDT (ppm)	DDD (ppm)	DDE (ppm)	ΣDDT (ppm)
1	Humpback whale	Pregnant female	Nova Scotia	5.4	ND	ND	4.7	3.4	15	23.1
2	Humpback whale	Juvenile male	New Jersey	6.0	0.2	1.2	3.3	1.0	3.3	7.6
3	Humpback whale	Juvenile male	Antigua	1.3	ND	ND	0.3	0.1	1.0	1.4
4	Humpback whale	Mature male	Saint Kitts	1.5	0.1	0.1	0.9	0.3	0.9	2.1
5	Sperm whale	Mature female	Anegada Passage	4.0	ND	ND	4.0	1.6	9.9	15.5
6	Sperm whale	Mature male	Anegada Passage	0.7	ND	ND	0.2	0.1	0.8	1.1
7	Sperm whale	Neonate female	Massachusetts	2.1	0.3	ND	3.7	0.6	4.6	8.9
8	Dense-beaked whale	Mature male	South Carolina	14	0.1	0.2	15	4.2	19	38.2
9	Dense-beaked whale	Juvenile male	New Jersey	29	0.3	0.3	35	8.1	22	65.1
10	Atlantic pilot whale	Old female	Rhode Island	114	1.4	3.0	54	27	187	268
11	Atlantic pilot whale	Juvenile male	Maine	42	0.6	1.1	5.3	4.0	21	30.3
12	Atlantic whitesided dolphin	Mature male	Nova Scotia	37	ND	1.4	13	3.7	24	40.7
13	Saddleback dolphin	Mature female	Rhode Island	69	1.2	2.6	23	9.9	38	70.9
14	Striped dolphin	Suckling female	Maryland	69	2.7	2.4	68	20	143	231
15	Striped dolphin	Mature male	Rhode Island	39	1.4	1.4	18	4.7	48	70.7
16	Harbor porpoise	Mature female	Rhode Island	74	2.6	1.5	28	9.5	20	57.5
17	Pacific white-sided dolphin	Mature female	California (held captive in New York)	147	5.0	4.1	82	63	878	1023
18	Pacific pilot whale	Juvenile female	California (captive)	46	ND	0.4	23	9.3	223	255.3

Table 3.1.6 (Table III of Harvey et al., 1974).

Table III. Chlorinated hydrocarbons in Denmark Strait[1] organisms.

Sample	Identification		Position North	Position West	Depth (m)	PCB (μg/kg)[2]	t-DDT μg/kg
1	Cod (Gadus morhua)	muscle...	65°45′	23°33′	90	2 (830)[3]	9 (1300)
		liver.....				730 (1900)	170 (440)
2	Shrimp (Pandalus borealis)..		65°53′	22°58′	0–200	18 (630)	1 (27)
3	Haddock (Gadus aeglefinus)	muscle...	65°48′	26°10′	230	–	3 (2900)
		liver.....				480 (1100)	260 (590)
4	Arctic Cod (Boreogadus saimarcki)	whole....	65°23′	21°15′	240	2100 (31,000)	9 (130)
5	Argentine (Argentina silus)	muscle...	65°23′	26°15′	240	19 (2,500)	6 (750)
		liver.....				1100 (10,000)	51 (470)
6	Wolf-fish (Anarhichas lupas)	muscle...	65°23′	26°16′	240	22 (4,500)	3 (530)
7	Halibut (Reinhardtius Hippoglossoides)	muscle...	66°15′	26°10′	570	68 (740)	21 (230)
		liver.....				96 (280)	330 (930)
8	Redfish (Sebastes marinus)	muscle...	66°15′	26°10′	570	360 (5600)	32 (500)
		liver.....				900 (3000)	190 (620)

[1] Collected in September 1971 from the Icelandic research trawler, Bjarni Saemundsson.
[2] All the samples contained mixtures of the three Aroclors, 1242, 1254 and 1260. The closest match was used for quantification.
[3] Concentrations in parentheses are on a lipid weight basis.

Table 3.1.7 (Table IV of Harvey et al., 1974).

Table IV. Chlorinated hydrocarbons in open North Atlantic pelagic fish[1].

Sample	Identification		Position North	Position West	PCB (μg/kg)	t-DDT μg/kg
1	Flying fish	whole....	31°	79°	50	7
2	Flying fish (Cypselurus exsilens)	muscle...	14°30′	10°18′	1.4 (410)[2]	0.6 (180)
3	Flying fish (Prognichthys rondeletii)	muscle...	30°	60°	4 (1500)	4 (1500)
4	Trigger fish (Canthidermis maculatus)	muscle...	19°30′	29°57′	1.9 (1900)	0.1 (120)
5	Dolphin (Coryphaena equiselis)	liver.....	17°47′	28°35′	1100 (21,000)	95 (2000)
6	Dolphin (Coryphaena hippurus)-	muscle...	25°06′	36°03′	10 (10,000)	3 (3300)
7	Shark (Carcharhinus longimanus)	liver.....	14°30′	22°17′	1200 (2500)	400 (820)
8	Silky shark	liver.....	31°	78°	5800 (13,000)	4800 (11,000)

[1] Collected during the winter of 1970–1971 with nets and by jigging.
[2] Concentrations in parentheses are on a lipid weight basis.

In Tables II–V the concentrations are presented in μg/kg (ppb) wet weight, and, in parentheses, μg/kg per lipid weight. Table V is graphically summarized in Figure 4 which shows average concentrations of PCBs and t-DDT in each genera.

Table 3.1.8 (Table V of Harvey et al., 1974).

Table V. Atlantic mesopelagic organisms.

No.	Identification	Date	Lat.	Long.	Depth	PCB (μg/kg)	t-DDT (μg/kg)
			A. Chauliodontidae				
1	Chauliodus danae	4/71	36°10'S	07°23'W	600	2.5 (210)[1]	2 (170)
2	" "	5/71	25°59'S	03°28'W	450	4 (580)	1 (170)
3	Chauliodus sloani	6/71	12°52'S	08°15'E	300	5 (800)	2 (270)
4	" "	11/70	14°50'N	25°34'W	660	14 (1,900)	5 (660)
5	Chauliodus danae	11/70	24°55'N	35°53'W	900	10 (1500)	5 (700)
6	" "	12/70	28°00'N	45°00'W	800	60 (7300)	12 (1,500)
7	Chauliodus sloani	7/9/72	34°54'N	15°03'W	700	10 (5,500)	2 (900)
8	" "	7/3/72	44°41'N	30°44'W	660	30 (760)	12 (300)
9	" "	8/1/72	51°25'N	20°21'W	725	42 (9,200)	12 (2,700)
10	" "	6/30 72	52°31'N	35°02'W	510	78 (2,200)	9 (250)
			B. Stomiatidae				
11	Stomias boa	7/12/72	33°55'N	18°11'W	110	34 (1,700)	7 (350)
12	" "	7/4/72	45°59'N	30°36'W	95	1 (4,500)	14 (7,000)
13	" "	6/25/72	48°29'N	48°44'W	90	67 (2,000)	16 (450)
14	" "	6/26/72	48°58'N	45°06'W	510	53 (2,200)	9 (380)
15	" "	8/1/72	51°25'N	20°21'W	725	28 (1,600)	11 (640)
16	" "	8/4/72	55°41'N	15°02'W	30	20 (540)	47 (1,200)
			C. Myctophidae				
17	Benthosema glaciale	7/23/72	38°19'N	19°28'W	50	45 (780)	-
18	" "	7/22/72	38°25'N	11°11'W	70	86 (700)	3 (25)
19	" "	7/3/72	44°41'N	30°44'W	660	73 (470)	4 (30)
20	" "	6/25/72	48°29'N	48°44'W	90	82 (470)	7 (40)
21	" "	6/26/72	49°00'N	44°54'W	650	72 (480)	6 (34)
22	" "	6/26/72	42°00'N	44°54'W	650	6 (40)	-
23	" "	6/30/72	52°31'N	35°02'W	510	170 (890)	17 (90)
24	" "	6/30/72	52°31'N	35°02'W	510	120 (700)	14 (82)
25	" "	8/4/72	55°41'N	15°02'W	30	70 (950)	0.5 (7)
26	" "	8/7/72	60°05'N	05°53'W	65	160 (1100)	10 (70)
27	" "	8/9/72	63°14'N	02°32'W	50	170 (1100)	29 (190)
28	Myctophum punctatum	6/25/72	48°30'N	48°37'W	55	110 (610)	10 (52)
29	Myctophum punctatum	6/30/72	52°31'N	35°02'W	510	54 (550)	3 (30)
30	Protomyctophum articulum	6/28/72	49°49'N	39°22'W	320	33 (540)	10 (170)
31	Protomyctophum articulum	6/30/72	52°23'N	34°51'W	390	74 (1,600)	11 (230)
32	Protomyctophum articulum	6/30/72	"	"	"	45 (1,600)	17 (600)
33	Ceratoscopelus warmingi	7/12/72	33°33'N	16°16'W	60	10 (140)	5 (78)
34	Ceratoscopelus warmingi	7/7/72	35°08'N	24°25'W	40	11 (280)	3 (85)

[1] Concentrations in parentheses are on a lipid weight basis.

Table 3.1.8 (cont.)

Table V (continued).

No.	Identification	Date	Lat.	Long.	Depth	PCB (μg/kg)	t-DDT (μg/kg)
35	Ceratoscopelus maderensis	7/6/72	37°28'N	26°38'W	75	16 (320)	6 (120)
36	Hygophum hygomi	7/9/72	34°44'N	21°33'W	40	–	2 (120)
37	" "	7/23/72	38°19'N	19°28'W	50	16 (380)	3 (70)
			D. Oplophoridae				
38	Acanthephyra haeckelii	5/71	34°28'S	16°13'E	750	6 (240)	3 (120)
39	Acanthephyra purpurea	7/72	34°54'N	15°03'W	700	30 (890)	17 (890)
40	Acanthephyra haeckelii	6/72	48°58'N	45°06'W	510	26 (230)	4 (37)
41	Systellaspis sp	4/71	34°09'S	42°52'W	200	14 (370)	8 (220)
42	Systellaspis debilis	11/70	15°30'N	26°20'W	90	9 (490)	3 (170)
43	" "	12/70	28°00'N	45°00'W	800	35 (1000)	6 (170)
44	" "	7/72	33°37'N	16°12'W	125	30 (1000)	5 (1700)
45	" "	7/72	36°13'N	25°33'W	760	36 (610)	12 (200)
46	" "	7/72	44°41'N	30°44'W	660	40 (710)	6 (100)
			E. Sternopthchidae				
47	Argyropelicus hemigymnus	7/72	35°10'N	18°56'W	660	22 (3,500)	4 (600)
48	Argyropelicus hemigymnus	7/72	36°12'N	15°45'W	600	28 (2,300)	6 (470)
49	Argyropelicus hemigymnus	7/72	42°17'N	29°59'W	130	66 (4,000)	11 (660)
50	Argyropelicus hemigymnus	7/72	44°01'N	22°06'W	370	28 (2,400)	7 (560)
51	Argyropelicus hemigymnus	7/72	44°54'N	22°07'W	510	37 (2100)	11 (650)
52	Argyropelicus Oolpheri	7/72	"	"	510	19 (440)	8 (180)
55	Argyropelicus hemigymnus	8/72	57°18'N	12°02'W	280	34 (1000)	11 (320)
			F. Gonostanomidae				
54	Cyclothone microdone	7/3/72	44°41'N	30°44'W	660	57 (5000)	8 (720)
55	Cyclothone microdone	6/30/72	52°31'N	35°17'W	510	41 (38,000)	14 (12,000)
56	Cyclothone microdone	8/5/72	58°10'N	11°29'W	650	140 (2,200)	20 (320)

that delivery processes of atmospheric pollutants are normal for those latitudes (Bowen et al., unpublished). It is possible to explain the low PCB value as produced by dilution with recently upwelled deep water and by rapid removal to the sediments because of the very high productivity of the area.

Table 3.1.9 (from Baird et al., 1975 - Table 2).

Table 2. Species, size distribution, migratory pattern, and concentration of chlorinated hydrocarbons in deep sea zooplankton and 1052 fishes of the Gulf of Mexico (M = vertical migrator; N = no extensive vertical migration.)

Station*	Depth (m)	Species	Number Individuals Processed	Mean Std. Length (mm)	Std. Length Range (mm)	WET WEIGHT DDE (ppm)	DDD (ppm)	DDT (ppm)	Dieldrin (ppm)	Total DDT (ppm)	1254 Aroclor† (ppm)	LIPID WEIGHT DDE (ppm)	DDD (ppm)	DDT (ppm)	Dieldrin (ppm)	Total DDT (ppm)	1254 Aroclor‡ (ppm)
1	00–160	*Notolychnus valdiviae* (M)	190	19	13–22	–	0.002	–	0.057	0.002	0.224	–	0.034	–	0.818	0.034	3.239
1	100–160	*Gonostoma elongatum* (M)	15	38	29–59	–	–	0.016	–	0.016	0.316	–	–	2.143	–	2.143	42.857
1	100–160	*Ceratoscopelus warmingi* (M)	20	37	21–59	–	0.004	–	0.026	0.004	0.065	–	0.198	–	1.385	0.198	3.463
1	290–380	*Cyclothone braueri* (N)	93	19	12–26	–	0.015	–	0.038	0.015	0.375	–	1.339	–	3.348	1.339	33.482
1	100–160	*Lepidophanes guentheri* (M)	6	47	38–57	–	0.004	–	0.004	0.004	0.085	–	0.054	–	0.476	0.544	10.870
1	100–160	Myctophidae (6 species) (M)	34	28	17–56	–	0.002	–	0.009	0.002	0.146	–	0.205	–	0.676	0.205	10.518
1	330–380	*Argyropelecus hemigymnus* (N)	27	24	10–30	–	0.015	–	0.018	0.015	0.350	–	1.539	–	1.795	1.539	35.897
1	Surface	*Gonichthys cocco* (M)	10	24	18–28	–	–	0.017	–	0.017	0.383	–	–	0.606	–	0.606	21.212
1	100–160	Plankton	–	–	–	–	0.001	0.003	–	0.002	0.040	–	0.042	0.253	–	0.295	3.370
2	60–130	*Notolychnus valdiviae*	48	19	13–22	0.014	0.008	0.060	0.120	0.162	0.926	0.201	1.272	0.870	1.740	2.343	13.387
2	110–180	*Gonostoma elongatum*	12	104	64–124	0.001	0.001	0.001	–	0.003	0.032	0.386	0.429	0.429	–	1.244	15.880
2	60–130	*Ceratoscopelus warmingi*	13	35	27–52	–	–	–	0.017	–	0.290	–	–	–	0.709	–	11.827
2	550–760	*Cyclothone* spp. (4 species) (N)	154	27	12–30	0.001	–	–	0.001	0.001	0.026	0.171	–	–	0.159	0.171	4.209
2	60–130	*Lampanyctus alatus* (M)	60	38	25–50	0.002	–	–	–	0.002	0.002	0.013	–	–	–	0.013	15.152
2	60–130	*Benthosema suborbitale* (M)	23	26	18–32	–	0.007	–	0.013	0.007	0.133	–	0.213	–	0.400	0.213	4.264
2	60–130	*Diaphus* spp. (*mollis* + *lutkeni*) (M)	8	35	25–46	0.004	–	–	–	0.004	0.275	0.194	–	–	–	0.194	13.579
2	Surface	Plankton	–	–	–	–	–	–	–	–	0.048	0.258	–	–	0.619	0.258	12.887
3	30– 75	*Gonostoma elongatum*	4	154	113–200	0.002	0.002	0.005	0.001	0.009	0.040	0.430	0.430	1.289	0.172	2.149	12.027
3	360–500	*Cyclothone* spp. (4 species)	129	27	12–30	–	0.002	–	0.001	0.002	0.033	–	0.199	–	0.099	0.199	4.313
3	80–120	Myctophidae (4 species)	13	40	28–63	–	0.007	–	0.017	0.007	0.158	–	0.182	–	0.456	0.182	3.418
3	Surface	Plankton	–	–	–	0.003	–	–	0.061	0.003	0.101	3.371	–	–	6.742	3.371	112.359
4	70–130	*Gonostoma elongatum*	14	103	81–120	0.0004	0.001	0.001	0.0002	0.002	0.023	0.169	1.208	1.208	0.604	2.585	9.903
4	490–650	*Cyclothone* spp.	123	27	12–30	–	–	0.001	0.003	0.001	0.032	–	–	0.169	0.395	0.169	4.794
4	70–130	*Lepidophanes guentheri*	12	54	44–66	–	0.006	–	–	0.006	0.052	–	0.628	–	–	0.628	5.499
4	625–710	*Lampanyctus alatus*	10	38	25–50	0.081	–	0.055	–	0.136	0.405	7.526	–	11.856	–	29.382	8.763
4	70–130	*Diaphus dumerili* (M)	16	42	26–49	–	0.001	–	0.010	0.001	0.033	–	0.043	–	0.363	0.043	4.313
4	70–130	*Diaphus* spp.	17	37	25–49	–	0.019	–	0.029	0.019	0.282	–	0.908	–	1.328	0.908	12.933
4	Surface	Plankton	–	–	–	–	–	–	–	–	0.075	0.307	0.307	3.067	1.227	3.681	42.945
5	Surface	Plankton	–	–	–	–	–	–	–	–	0.157	–	0.205	–	–	0.205	19.087

* Station 1—27°00'N 86°00'W; Station 2—27°30'N 88°30'W; Station 3—29°19'N 87°01'W; Station 4—28°35'N 89°00'W; Station 5—29°26'N 87°17'W.
† Wet weight reagent blank 0.004 ppm.
‡ Lipid weight reagent blank 100.00 ppm.

Table 3.1.10 (from Fowler and Elder, 1978 - Table 4).

TABLE 4

PCB RESIDUES IN MIXED PLANKTON FROM DIFFERENT OCEANIC AREAS

Region	*Date*	*Net mesh Size*	*Mean (range) µg/kg wet*	*Reference*
NW Atlantic shelf	1969, 1971	239	91·2[a] (7·1–300)	Risebrough *et al.* (1972)
North Atlantic	1970	239	380 (300–450)	Risebrough *et al.* (1972)
South Atlantic	1971	239	200 (16–640)	Risebrough *et al.* (1972)
North and south Atlantic	1970–1972	239	200 (≃10–1000)	Harvey *et al.* (1974*a*)
North-east Atlantic	1971	—	60 (10–110)	Holden (1972)
Firth of Clyde	1971	—	485 (40–2200)	Holden (1972)
Stockholm archipelago	1971	100	— (3–350)[b]	Jensen *et al.* (1972)
Gulf of St Lawrence	1972	73	1390 (90–3050)	Ware & Addison (1973)
Gulf of St Lawrence	1972	239	700 (N.D.–1860)	Ware & Addison (1973)
South-west coast of Finland	1972–1973	150	190 (40–750)	Linko *et al.* (1974)
South-west coast of Finland	1974	150	370 (30–3300)	Linko *et al.* (1979)
South-west coast of Finland	1976	150	230 (40–720)	Linko *et al.* (1979)
Gulf of Mexico-North Caribbean	1971	239 or 750	95 (<3–1055)	Giam *et al.* (1973)
Gulf of Mexico	1973	333	84 (40–157)	Baird *et al.* (1975)
North-east Pacific	1973–1975	333	40 (≃1–180)	Clayton *et al.* (1977)
Eastern Mediterranean	1977	239	7 (2–25)	Present study

[a] Converted at dry:wet weight = 10%.
[b] Converted at fat:wet weight = 1%.

Table 3.1.11 (from Butler et al., 1983 - Table 11-1).

Table 11-1
Average Concentrations (μg/g – Dry Weight) of Nonpolar Hydrocarbons in Members of the Pelagic Sargassum Community

Organism (number of samples)	*n-Alkanes*		*Unresolved Envelope*	*Total*	*Petroleum/ Biogenic*
	Biogenic	*Petroleum*			
Sargassum natans (37)	1.4[a]	5.2	17.6	23.1	16.3
Sargassum fluitans (10)	0.8[b]	3.3	7.8	12.3	13.9
Litiopa melanostoma (4)	0.3[c]	4.4	3.2	8.1	25.3
Scyllaea pelagica (1)	40.5	420	104	619	12.9
Latreutes fucorum (4)	0.2[d]	50.3	82.0	135	132.5
Leander tenuicornis (2)	7.2[d]	18.1	51.2	77.7	44.6
Planes minutus (5)	0.6[d]	2.5	13.1	16.5	26.0
Portunus sayi	0.8[d]	109	381	500	612.1
Syngnathus pelagicus	34.9[d]	1466	1764	3411	92.6
Carangidae ("Jacks")	3.5	21.2	53.9	81.0	21.2
Mixed Fauna	2.3	45.9	31.3	83.1	33.6

[a] C_{15}, 0.2, C_{17}, 1.0, C_{19}, 0.2.
[b] C_{15}, 0.3, C_{17}, 0.5.
[c] C_{15}, 0.1, C_{17}, 0.2.
[d] Principally C_{17}.

Table 3.1.12 (from Butler et al., 1983 - Table 11-2).

Table 11-2
Hydrocarbon Levels (μg/g Dry Weight) in Various Members of the Pelagic Sargassum Community

Organism	*Dry/Wet Weight Ratio*	*Number of Samples*	*Biogenic*	*Petroleum*	
Sargassum natans algae	0.23	37(12)	1.4(7.7)	22.8(10.6)	16(1.4)
Sargassum fluitans algae	0.17	10(1)	0.8(69.4)	11.1(13.2)	14(0.2)
Planes minutus crab	0.22	5(1)	0.6(0.0)	15.6(49.5)	26(–)
Portunus sayi crab	0.19	3(1)	0.8(0.0)	490(177)	613(–)
Syngnathus pelagicus pipefish	0.27	2(1)	35(1)	3230(32.6)	93(31)
Leander tenuicornis shrimp	0.14	2(1)	7.2(1.1)	69.3(20.4)	45(18)
Histrio histrio fish	0.25	–(1)	–(0.2)	–(0.5)	–(31)
Canthidermus sp fish	0.25	–(1)	–(0.3)	–(1.0)	–(21)
Litiopa melanostoma[a] snail	0.04	4(–)	7.5(–)	190(–)	25(–)
Scyllaea pelagica nudibranch	0.03	1(–)	40.5(–)	524(–)	13(–)
Latreutes fucorum shrimp	0.11	4(–)	0.2(–)	132(–)	133(–)
Carangidae sp. fish	0.18	1(–)	3.5(–)	75(–)	21(–)
Mixed Fauna	0.16	3(–)	2.3(–)	77(–)	34(–)

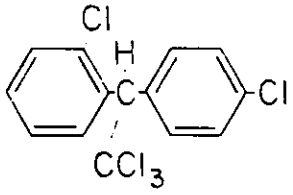
NOTE: The present data is compared to the results reported by Burns and Teal (1973) given in parentheses.

Table 3.1.13 (from Burns and Teal, 1973 - Table 2).

Table 2. Hydrocarbons found in Sargasso plants and animals. Values all in μg/g wet weight (PPM).

Sample	*Description*	*Position collected*	*Natural*	*Petroleum n-Alkane*	*Petroleum Unresolved*	*Petroleum natural*
1. (25·3 g)	*S. natans*	31°59'N 63°27·5'W	1·38	0·36	4·72	3·7
2. (25·6 g)	(narrow blade)	31°29'N 62°23'W	0·55	0·16	1·71	3·4
3a. (26·4 g)	,, ,,	30°22'N 60°46'W	0·58	0·18	1·59	3·0
b. (Pentane washings)	,, ,,		(0·03)	(0·07)	(0·21)	(9·3)
4. (40·4 g) (new fronds)	,, ,,	31°43'N 62°35'W	0·51	0·06	1·21	2·5
5a. (26·0 g)	,, ,,	30°22'N 60°46'W	1·84	0·36	3·57	2·1
b. (Pentane washings)	,, ,,		(0·06)	(0·09)	(0·97)	(17)
6. (46·4 g) (old fronds)	,, ,,	31°43'N 62°35'W	0·68	0·05	1·28	1·9
7. (26·4 g)	,, ,,	31°59'N 63°27·5'W	0·78	0·33	0·99	1·7
8. (32·7 g)	,, ,,	31°43'N 62°35'W	2·11	0·23	2·71	1·5
9a. (25·6 g)	,, ,,	30°22'N 60°46'W	2·36	0·30	2·68	1·3
b. (Pentane washings)	,, ,,		(0·06)	(0·24)	(1·62)	(31)
10. (41·7 g)	,, ,,	31°59'N 63°27·5'W	4·28	0·44	3·16	0·84
11a. (25·9 g)	,, ,,	30°22'N 60°46'W	2·32	0·12	1·69	0·77
b. (Pentane washings)	,, ,,		(0·50)	(0·08)	(0·40)	(0·96)
12. (37·2 g)	,, ,,	35°19'N 63°56'W	3·73	0·15	1·03	0·32
13. (34·8 g)	(wide blade)	35°19'N 63°56'W	11·8	0·19	2·05	0·19
14. 4 crabs (2·94 g)	*Planes minuta*	31°59'N 63°27·5'W	0·00	0·28	10·60	∝
15. 4 crabs (1·18 g)	*Portunus sayi*	35°19'N 63°56'W	0·00	8·22	25·48	∝
16. 18 *Sargassum* fish (8·76 g)	*Histrio histrio*	35°19'N 63°56'W	0·05	0·13	1·45	31
17. 13 pipefish (2·44 g)	*Syngnathus pelagicus*	,, ,,	0·27	1·41	7·39	31
18. 1 triggerfish (7·42 g)	*Canthidermis sp.*	,, ,,	0·08	0·26	1·41	21
19. 53 *Sargassum* shrimp (7·35 g)	*Leander tenuifornis*	,, ,,	0·16	0·51	2·35	18

ORGANOCHLORINE STRUCTURES



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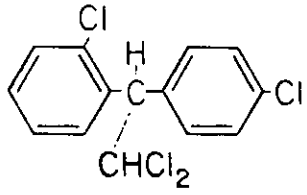

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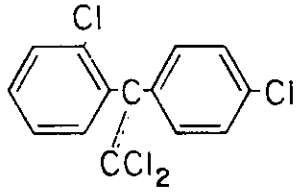

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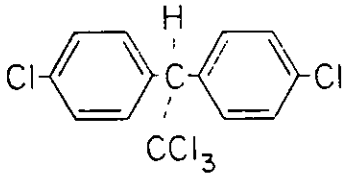

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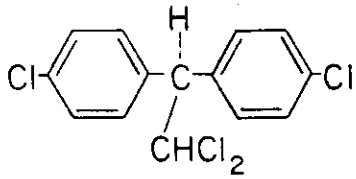

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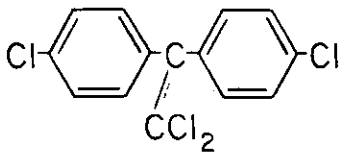

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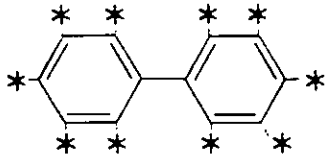
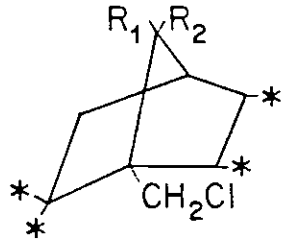


PCB

* Cl *may be substituted at various positions, 209 possible molecular configurations*

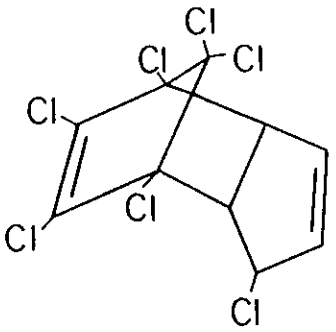


Toxaphene

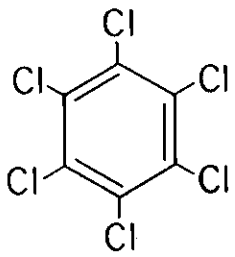
* Cl *may be substituted at various positions; Toxaphene is a poorly characterized mixture of Chlorinated Camphenes*

Figure 3.1.1 Structures of organochlorine pesticides and PCBs.

heptachlor



hexachlorobenzene



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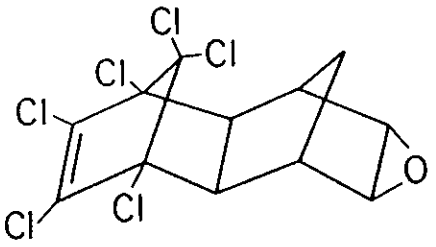
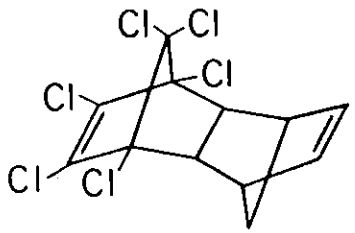
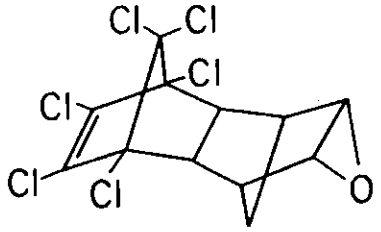




aldrin

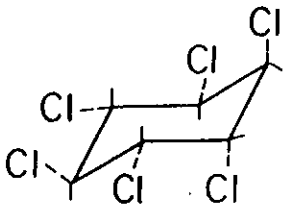


dieldrin

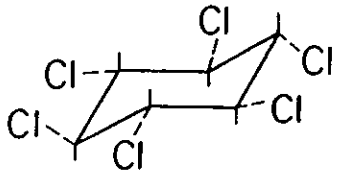
Figure 3.1.1 (continued)

CYCLOHEXANE

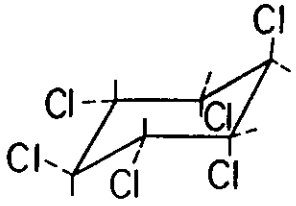
alpha

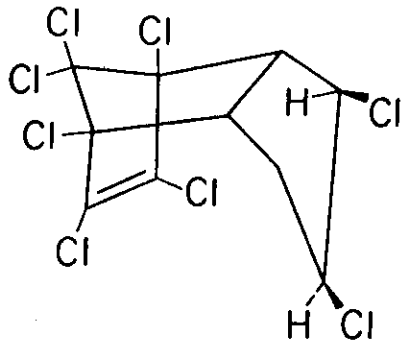


beta

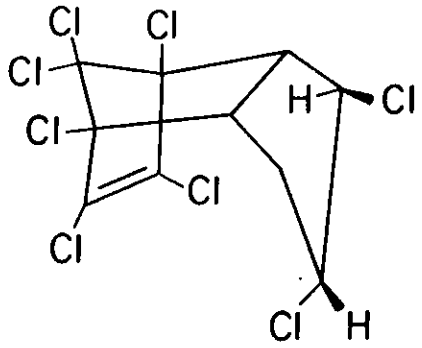


gamma





alpha



gamma

CHLORDANE

Figure 3.1.1 (continued)

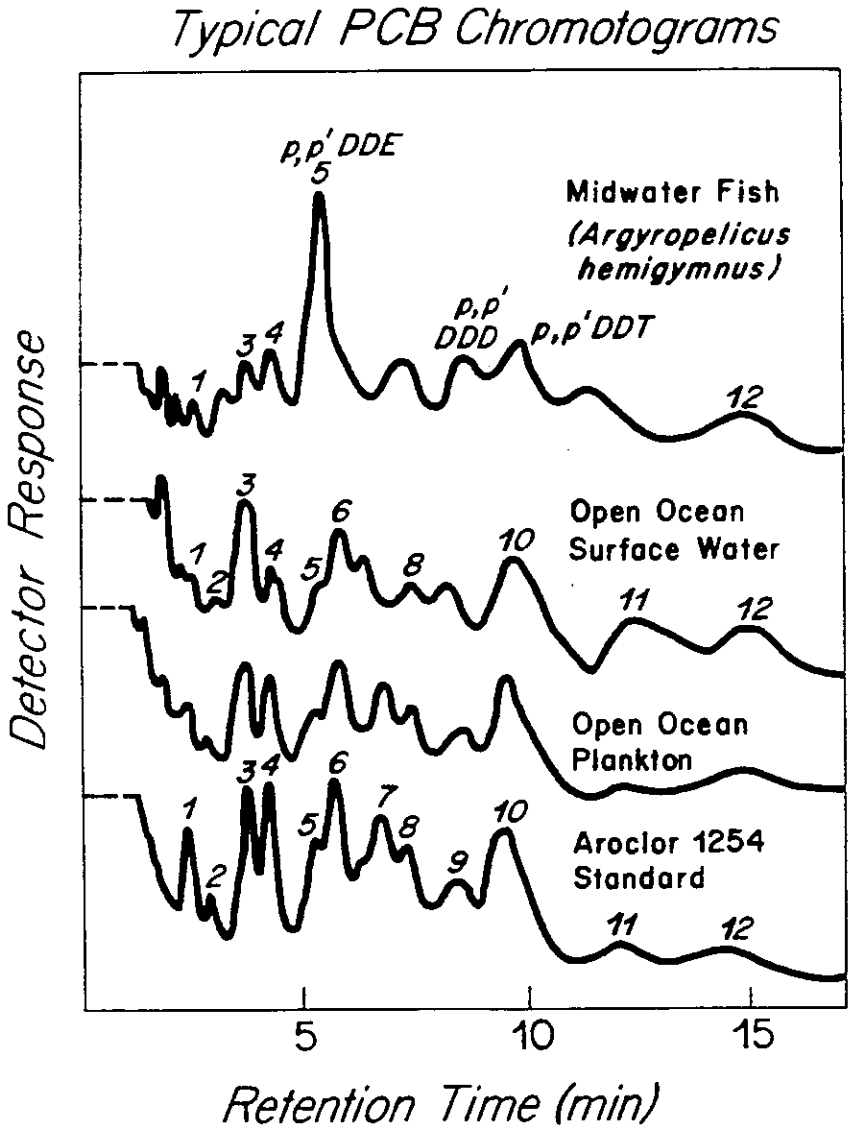


Figure 3.1.2 Examples of packed column GC analyses of organochlorine pesticides and PCBs (from Harvey et al., 1974).

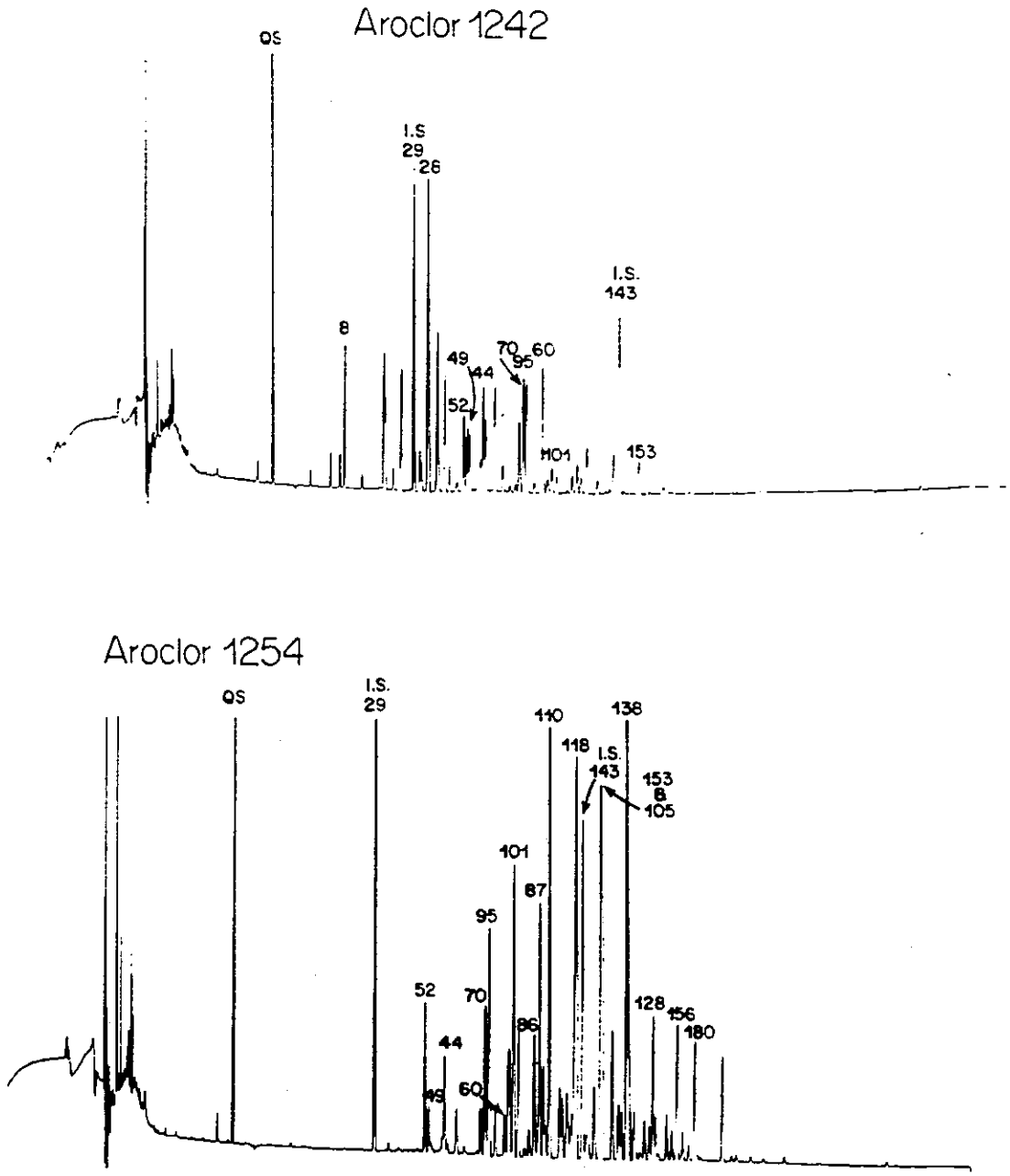


Figure 3.1.3a Capillary gas chromatograms (electron capture detector) of Aroclor PCB mixtures. QS designates quantitation standard. I.S. designates internal standard. Numbers designate individual chlorobiphenyls by IUPAC code.

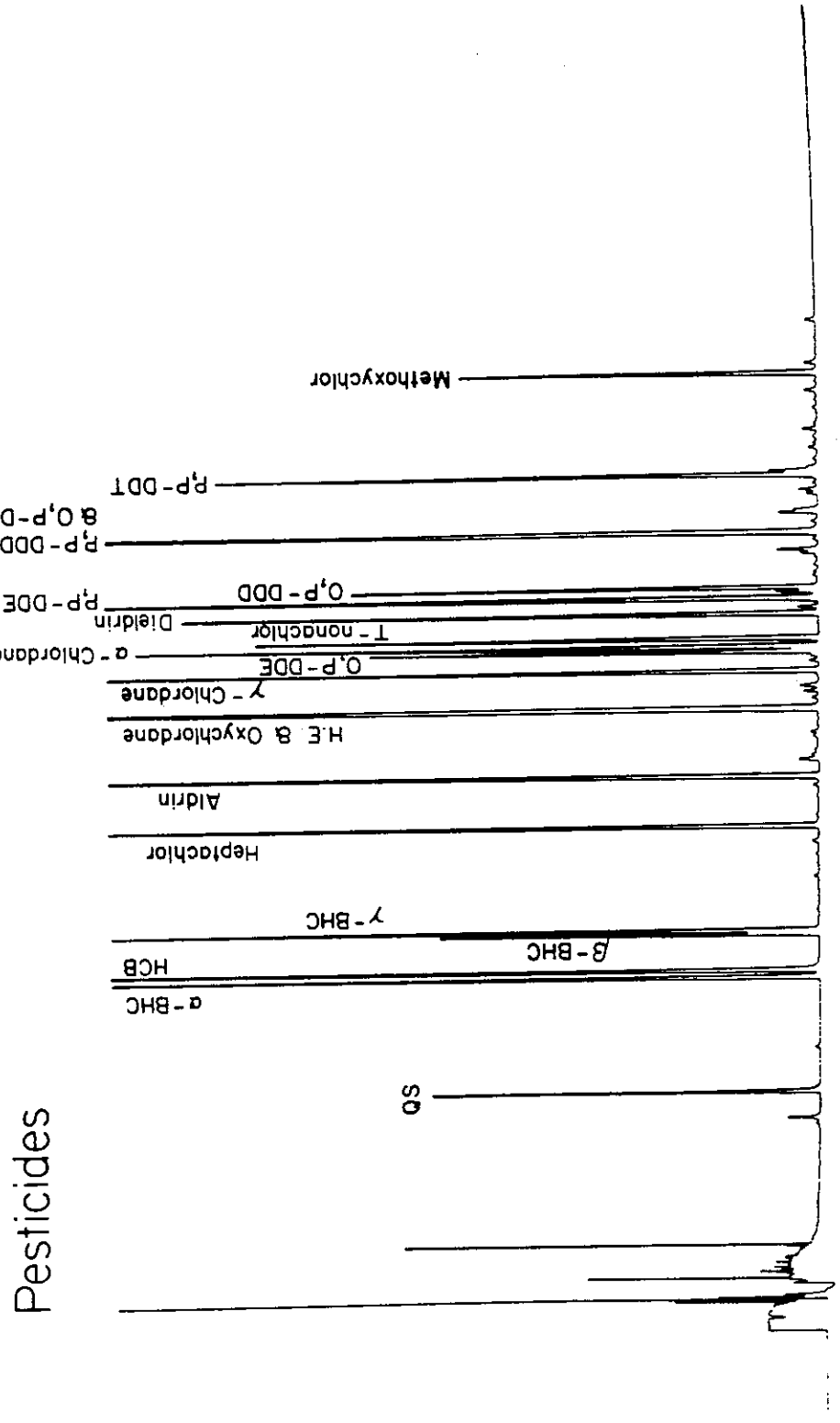


Figure 3.1.3b Capillary gas chromatogram (electron capture detector) of organochlorine pesticide mix.

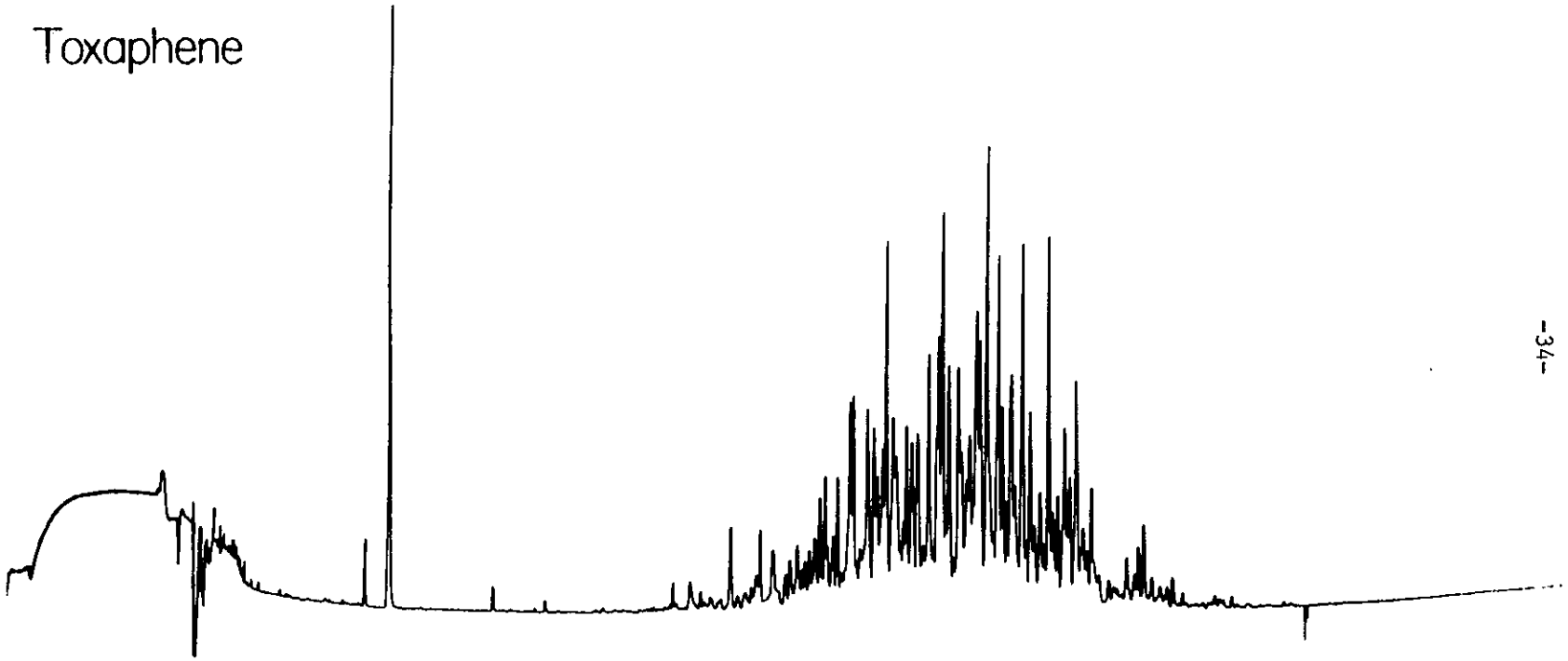


Figure 3.1.3c Capillary gas chromatogram (electron capture detector) of Toxaphene.

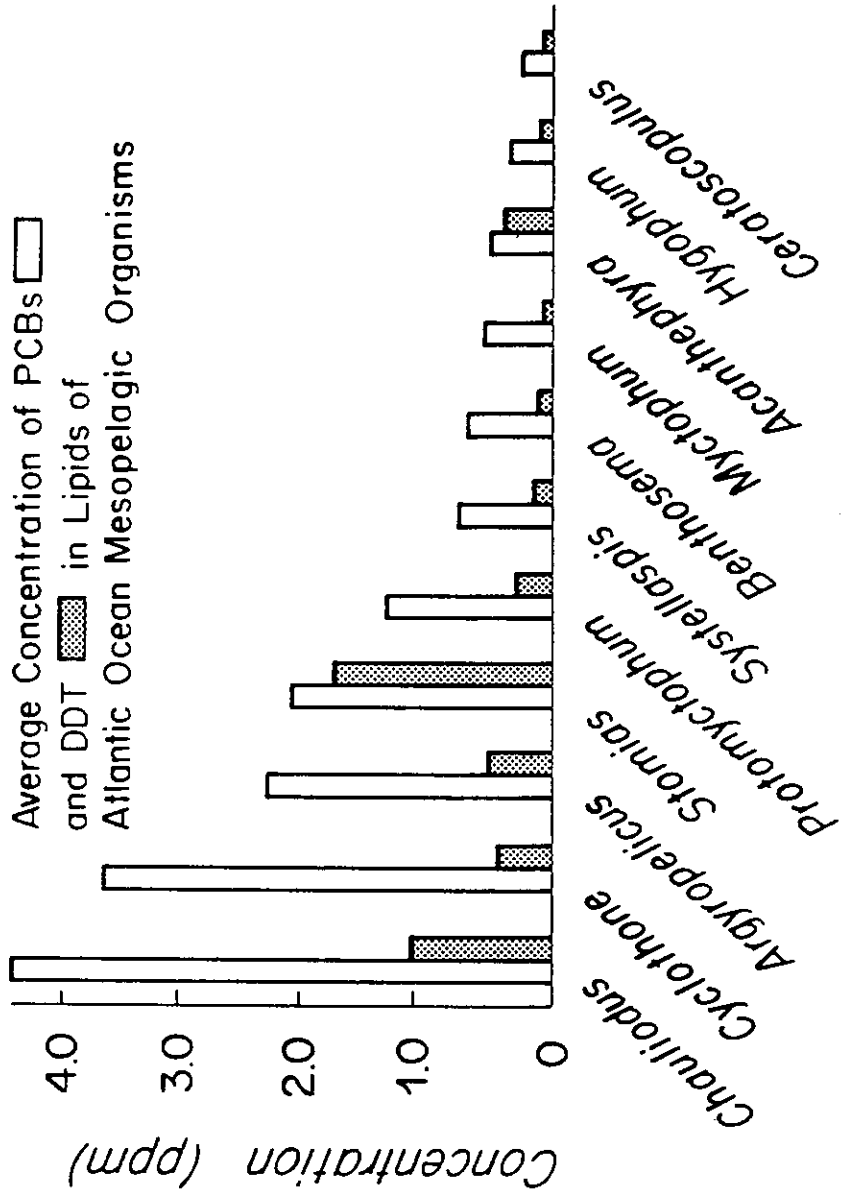


Figure 3.1.4 Data from Harvey et al., 1974 (Figure 4).

III. 2. Body Burden Data for Organochlorines in Deep Sea Fish: Results of New Analyses Completed for this Project

The sampling of fish and the locations of collections are given in Section IIIB of this report, by Dr. John Stegeman and in Table 3.2.2.

Methods of Analysis

Approximately 1 g of wet liver tissue was digested with 4 N NaOH overnight at 30°C. PCBs and chlorinated pesticides were extracted from the aqueous digestate with ethyl ether, concentrated and partitioned between hexane and methanol/water. PCBs and pesticides were isolated from extracted lipids by column chromatography using 5% deactivated alumina over 5% deactivated silica gel. The column was first eluted with hexane and then PCBs and pesticides were collected in the second fraction eluted with 20% toluene in hexane. The pesticide fraction was concentrated to a small volume. Initial screening by packed column gas chromatography was done for several samples on a Perkin Elmer Model 900 GC with Ni-63 electron capture detector equipped with a 3 meter glass column coated with 1.95% OV-17/1.5% QF-1. All samples were analyzed by glass capillary gas chromatography on a commercially available 0.35 mm i.d. x 30 meter SE-52 column (J & W Scientific Company) installed in a Carlo Erba Model 2150 gas chromatograph equipped with a split/splitless injector and Ni-63 electron capture detector. The gas chromatograph was interfaced with a Columbia Scientific Instruments Company Supergrator 3 electronic integrator. Carrier gas was maintained at 0.5 kg/ cm^2 of H_2. Temperature conditions started with on-column injection at 70°C, followed immediately by rapid heating to 130°C and then programmed to 270°C at 2°/minute.

Internal standards were added to the digestion extraction mixture at initiation of extraction: 2,4,5-trichlorobiphenyl (IUPAC No. 29) and 2,2',3,4,5,6'-hexachlorobiphenyl (IUPAC No. 143). Response factor curves for the electron capture detector were generated for the chlorobiphenyl isomers listed in Table 3.2.1.

The amount of total Aroclor 1242 or 1254 in a standard solution was ratioed against the amount of individual isomers within the mix to give an Aroclor Conversion Factor (ACF). Several ACFs were calculated from separate chromatographic runs to produce an average ACF. The average ACF is used to estimate an equivalent amount of Aroclor based on the amount of individual isomer present in the tissue samples. Isomers 8 and 28 are used to estimate 1242; isomers 101, 87, 153, 138 are used to estimate 1254; and isomers 52, 44, 70, found in both mixtures, give a combined 1242 + 1254 equivalent amount. Samples which have undergone only small changes in their Aroclor composition will yield consistent equivalences. If some process has produced an altered Aroclor composition (e.g. metabolism) a sample may show Aroclor equivalences that are inconsistent. This was the case with the benthic fish and will be discussed. PCBs were then calculated as Aroclor mixtures from the calibration curves based on data from glass capillary gas chromatograpic analysis for each sample.

Individual chlorobiphenyls were quantified by high resolution gas chromatography using response curves generated by analyses of a standard of each chlorobiphenyl. Recoveries of internal standards were variable at 50 to 97%.

Electron impact (EI) and positive/negative ion chemical ionization (PNICI) mass spectra were obtained using a Finnigan 4510 quadrupole mass spectrometer equipped with a standard EI/CI ion source and a PPINICI (pulsed positive ion

negative ion chemical ionization) accessory. Methane (Matheson UHP, 99.97%) was used as the reagent gas at a source pressure of 0.75 torr (uncorrected). The electron energy was 70 eV for electron impact ionization and 100 eV for chemical ionization. The emission current was 350 uA. The ion source temperature was 100°C and the manifold temperature was 95°C. Pre-amplifier sensitivity was set at 10^{-7} A/V, the electron multiplier voltage was 1.2 kV and the conversion dynode voltages were +/- 3.0 kV.

Data were acquired using a Finnigan INCOS 2300 data system. Scan times were 0.95 sec (m/z 50-650) for electron impact spectra, 0.5 sec (m/z 100-650) for positive ion CI and 0.5 sec (m/z 50-650) for negative ion CI. Additional sensitivity was obtained by operation in negative ion CI mode only, using 0.95 sec scans from m/z 50-650.

Samples were introduced via a Carlo Erba 4160 gas chromatograph interfaced directly to the mass spectrometer using a fused silica capillary column. The column was a 25 m x 0.32 mm i.d. DB-5 bonded phase fused silica column (J & W Scientific). The carrier gas was helium at a pressure of 0.8 atm. Samples were injected on-column at 80°C and, after a 3-minute hold-time, the column was programmed from 80-130°C at 20°C/min and then to 310°C at 3°C/min.

Results and Discussion

The results of analyses tabulated to date are presented in Tables 3.2.2, 3.2.3 and 3.2.4. Quantitative data for organochlorine compounds other than DDE and PCBs will require further analysis. However, we do know from tentative identification by GC and GCMS that hexachlorobenzene, Toxaphene, and chlordanes are present.

We find concentrations of DDE and PCBs are in the range of those reported for A. rostrata by Barber and Warlen (1979) - see Table 3.1.2 and Risebrough

et al. (1976) Table 3.1.3. The agreement among data from individuals of the same species is reasonable and similar to that expected for coastal organisms (Phillips, 1980). The data for the different species caught in the same location at the same time (Oc 126 samples) show some differences in concentration for DDE but the total number of samples is small, making the assessment of the significance of differences difficult.

The glass capillary gas chromatographic analyses are illustrated in Figures 3.2.1, 3.2.2, 3.2.3. The glass capillary gas chromatograms from livers of the same species C. armatus sampled at Site I and Site II (see Stegeman, Section IIIB) show striking similarities in the relative ratios of DDE and the most abundant chlorobiphenyl isomers. We have quantitatively analyzed for individual chlorobiphenyls in livers of C. armatus at Site I and Site II since this is the only species for which we have samples at each site. We have standards for the limited number of chlorobiphenyls given in Tables 3.2.3 and 3.2.4. The patterns of chlorine substitution are given in Table 3.2.4 with corresponding IUPAC (International Union of Pure and Applied Chemistry) code numbers. Although there are only two samples for Site II and five samples for Site I there are significant differences for several chlorobiphenyls when comparing the two sites. The cause of the differences in concentrations of the chlorobiphenyls and the differences in DDE concentrations (Table 3.2.2) cannot be elucidated at this time. The proximity of Site I near the Hudson Canyon, which is seaward of a continental shelf adjacent to the industrialized United States northeast megapolis coast and the remoteness of Site II from similar conditions, tempts us to speculate that some offshore transport of organochlorine compounds occurs near the Hudson Canyon. However,

we emphasize that this sort of speculation can be, at the very best, considered a testable hypothesis and no more should be extrapolated from the limited number of, and types of, samples we have analyzed.

A comparison of the chromatograms in Figure 3.2.1 with those for PCBs (Aroclor 1254) in Figure 3.1.3 illustrates another major finding for these data. Chlorobiphenyl mixtures found in all the fish livers are severely altered compared to the Aroclor mixtures originally released to the environment. The pattern of chlorine substitutions found on the biphenyls has been hypothesized as the primary reason for selective degradation of PCB isomers (Ballschmiter et al., 1981). Data of Stegeman (Section IIIB) showing the presence of enzyme activity of the type that might be capable of metabolizing some of the chlorobiphenyls is consistent with our finding that the composition of PCBs is altered in the fish compared to Aroclor industrial mixtures.

The changes in relative abundance of chlorobiphenyls in fish livers in comparison to the Aroclor industrial mixtures means that the estimates of Aroclor mixture concentrations (Table 3.2.2) could be in error by a substantial (but unknown) margin. At best Table 3.2.2 Aroclor estimates are estimates of concentrations that would be found in the livers if selective uptake or metabolism did not alter composition. Our reason for attempting such a calculation for this report was to provide a rough estimate of Aroclor concentrations, especially Aroclor 1254, to compare with packed column GC estimates of Aroclor 1254 in similar samples analyzed by other investigators several years ago as discussed earlier.

The gas chromatograms in Figure 3.2.2 illustrate that analyses of livers from three different fish of the same species yield the same general pattern.

Apparent differences for the bottom chromatogram result from detector signal magnification and injection of more sample material in order to enhance signal peaks for some of the minor components.

Organochlorines in livers from three different species caught at the same site at approximately the same time are seen in the gas chromatograms in Figure 3.2.3 . In this figure some differences in composition between these chromatograms probably indicate species specificity in either uptake, metabolism, or excretion. The pattern of the chromatogram suggests the presence of Toxaphene (see Figure 3.1.3b) and is similar to that reported by Ballschmiter and coworkers in fish livers from fresh water lakes, oceanic surface waters and nearshore areas (Ballschmiter et al., 1981; Zell et al., 1980a,b; Krämer et al., 1984). Given the probable presence of Toxaphene identifications of individual chlorobiphenyls by GC alone are somewhat tenuous. Thus we undertook GC/MS analyses.

Representative GC/MS plots from the PPINICI analyses are presented in Figures 3.2.5 to 3.2.10. The top plot in each case is the positive ion plot; the bottom plot is the negative ion plot for computer reconstructed total ion chromatograms. A detailed explanation of the PPINICI procedure is beyond the scope of this report. PCBs give a stronger response to methane chemical ionization yielding positive ions and some pesticides such as Toxaphene give a stronger response to methane chemical ionization yielding negative ions (Figures 3.2.5 and 3.2.10). It is sufficient for our purposes to state that PPINICI helps to resolve some of the problems of identification of individual peaks and that these data demonstrate a higher abundance of Toxaphene relative to PCBs in the Oc 126 samples compared to the OC 93 samples. This difference

can be visualized by comparing the relative peak heights of the top plot in each figure which enhances the signal for PCBs and the bottom plot in each figure which enhances the signal for Toxaphene.

There are indications of the presence of Halowax compounds (polychlorinated naphthalenes) in the fish livers based on initial interpretations of the GC/MS data. Further data interpretation of the GC and GC/MS results is needed to obtain the full set of information for this unique set of analyses and we are continuing this work.

High resolution glass capillary GC and PPINICI GC/MS analyses document the presence of DDE, PCBs, and Toxaphene in livers of rattails of the continental slope off North America. The distribution of PCB isomers clearly indicates that metabolism or some other factor such as selective uptake and release has altered the original composition of PCBs. The resulting PCB distribution is similar to that reported for fishes and crustacea in the nearshore. The concentrations and composition of organochlorine compounds in fish livers depends on a number of factors: i) concentration and composition of compounds in the food and habitat of the fish; ii) level of enzyme activity capable of metabolizing the compounds; iii) time between capture and the last meal. Given these factors, it is not surprising that data for individual chlorobiphenyls in livers from several individual fish caught at the same time at the same location exhibit the variability reported in Tables 3.2.3 and 3.2.4.

Table 3.2.1

Aroclor Conversion Factor (ACF) ng Aroclor/ng chlorobiphenyl

Injection #	Aroclor 1242 376	416	487	585	Aroclor 1254 377	417	485	562	ACF Average
Chlorobiphenyl #									
8	13.2	14.0	12.9	13.2	--	--	--	--	13.3
28	8.9	9.0	7.9	8.8	--	--	--	--	8.6
52	42.0	41.5	41.3	40.7	27.6	28.7	26.4	27.9	34.5
44	21.4	28.6	26.9	26.2	42.7	39.5	41.8	37.7	33.1
70	28.2	30.4	28.7	27.9	29.5	31.9	29.4	30.2	29.5
101	--	--	--	--	11.9	12.6	11.5	12.1	12.0
87	--	--	--	--	19.8	22.2	20.2	20.9	20.8
153	--	--	--	--	11.5	11.5	11.8	12.3	11.7
138	--	--	--	--	11.9	12.2	12.0	12.4	11.9

Injection #	Aroclor 1268 389	485	593	ACF Average
Chlorobiphenyl #				
195	7.2	8.9	8.4	8.2
207	18.9	31.8	29.4	26.7
194	17.6	21.8	20.7	20.0
206	3.0	2.9	2.8	2.9
209	11.4	13.1	12.4	12.3

Table 3.2.2

PCB and DDE concentrations in livers of deep sea fish (rattails) caught in the northwest North Atlantic Ocean.

Sample	10^{-6} g/g wet weight				
		PCB Aroclor Mixture			
	p,p'DDE[a]	1242	1254	1268	Total
Site I - Near Hudson Canyon					
Oc-93 Trawl 900					
3/28/81					
38°35'N, 69°58'W					
3245 meters					
Coryphaenoides armatus					
Fish #1	2.11	0.115	2.35	.307	2.77
Fish #2	1.62	ND[b]	1.69	.225	1.92
Fish #3	1.76	ND	5.38	.645	6.03
Fish #5	2.51	0.064	4.80	.738	5.60
Fish #6	2.51	0.066	5.36	.710	6.14
Site II - Near Carson Canyon					
OC-126 Trawl 1363					
9/13/82					
45°16'N, 48°34'W					
Coryphaenoides armatus					
Fish #3	0.371	0.029	0.932	0.183	1.14
Fish #8	0.162	0.028	0.316	0.027	0.37
Trawl 1363					
Coryphaenoides rupestris					
Fish #3	0.15	0.135	0.645	ND	0.78
Fish #4	0.15	0.072	0.577	ND	0.65
Antimora rostrata					
Fish #1	1.28	0.220	3.51	ND	3.73
Fish #2	2.57	0.434	6.71	ND	7.14
Fish #4	0.687	0.368	2.39	ND	2.86
Analytical Blanks					
#1	ND	ND	ND	ND	--
#2	ND	0.017	ND	0.017	--

[a]Total DDT and DDE

[b]ND < 0.01

Table 3.2.3

Chlorobiphenyl concentrations in C. armatus livers from fish in Hudson Canyon and Carson Canyon areas.

(10^{-9} g/g wet weight)

Chlorobiphenyl IUPAC No.	Hudson Canyon* 1	2	3	5	6	Carson Canyon* 3	8
28	13.1	N.D.	N.D.	7.4	7.7	3.4	3.2
52	13.7	9.7	86.1	54.1	70.4	11.7	5.2
49	30.7	6.8	59.3	23.8	16.4	17.1	2.6
44	N.D.	N.D.	103	12.0	N.D.	N.D.	1.2
70	10.8	7.5	30.1	18.0	25.3	7.5	2.7
95	80.7	40.9	273.1	80.3	141	9.5	8.1
60	8.1	6.0	11.0	4.4	13.9	5.5	1.2
101	78.0	43.9	209.3	346	323	83.4	20.8
86	24.7	8.1	25.8	78.5	N.D.	N.D.	6.4
87	N.D.	12.1	26.1	12	29.1	4.1	9.3
153	342	243	829	808	631	117	37.1
105	76.1	59.0	180	185	145	10.5	9.3
141	11.3	7.9	32.2	22.4	3.0	2.2	5.3
137	27.6	18.5	51.8	79.5	50.0	6.4	4.7
138	369	259	723	839	791	105	32.0
129	20.8	19.9	62.2	176	61.9	9.40	2.6
183	52.7	40.9	136	270	100	15.5	6.0
128	8.4	5.6	31.6	132	19.1	1.07	6.5
156	42.1	26.6	80.5	63.2	56.0	8.6	5.5
180	244	160	491	444	420	58.1	33.2
195	18.7	13.3	40.6	121	108	10.2	6.0
207	6.7	4.6	15.3	11.7	13.1	1.7	0.38
194	39.2	29.2	81.3	73.6	71.2	8.7	2.1
206	39.0	29.1	73.1	60.4	62.1	7.4	2.2
Total**	1820	1060	3690	3920	3160	504	215

*Individual fish.
**Total of measured individual chlorobiphenyls.

Table 3.2.4

Chlorobiphenyl concentrations in C. armatus livers from fish in Hudson Canyon and Carson Canyon areas. Values are in 10^{-9} g/g wet weight and are given as means ± one standard deviation. The data were analyzed by the t-statistic as in Table 1. Asterisk indicates differences significant at $P < 0.05$. Compilation from Table 3.2.3.

Chlorobiphenyl IUPAC No.	Substitution Pattern	Hudson Canyon Area (N=5)	Carson Canyon Area (N=2)
28	2,4,4'	6 ± 6	3.3 ± 0.1
44	2,2',3,5	23 ± 45	0.6 ± 0.8
49	2,2',4,5	27 ± 20	10 ± 10
52	2,2',5,5	47 ± 34	8.5 ± 4.6
60	2,3,4,4'	9 ± 4	3.4 ± 3
70	2,3',4',5	18 ± 9	5.1 ± 3.4
86	2,2'3,4,5	27 ± 31	3.2 ± 4.5
87	2,2',3,4,5'	16 ± 12	6.7 ± 3.7
95	2,2',3,5',6	123 ± 91	8.8 ± 1.0
101	2,2',4,5,5'	200 ± 140	52 ± 44
105*	2,3,3',4,4'	129 ± 59	9.9 ± 0.9
128	2,2',3,3',4,4'	44 ± 60	3.8 ± 3.8
129	2,2',3,3',4,5	68 ± 64	6.0 ± 4.8
137*	2,2',3,4,4',5	46 ± 24	5.6 ± 1.2
138*	2,2',3,4,4',5'	596 ± 264	69 ± 52
141	2,2',3,4,5,5'	15 ± 12	3.8 ± 2.2
153*	2,2',4,4',5,5'	570 ± 268	77 ± 57
156*	2,3,3',4',4',5	54 ± 34	7.1 ± 2.2
180*	2,2',3,4,4',5,5'	352 ± 142	46 ± 18
183*	2,2',3,4,4',5',6	120 ± 92	11 ± 7
194	2,2',3,3',4,4',5,5'	59 ± 24	5.4 ± 5.0
195	2,2',3,3',4,4',5,6	60 ± 51	8.1 ± 3.0
206*	2,2',3,3',4,4',5,5',6	53 ± 18	4.8 ± 4.0
207*	2,2',3,3',4,4',5,6,6'	10 ± 4	1.0 ± 0.9
Total*		2730 ± 1240	360 ± 204

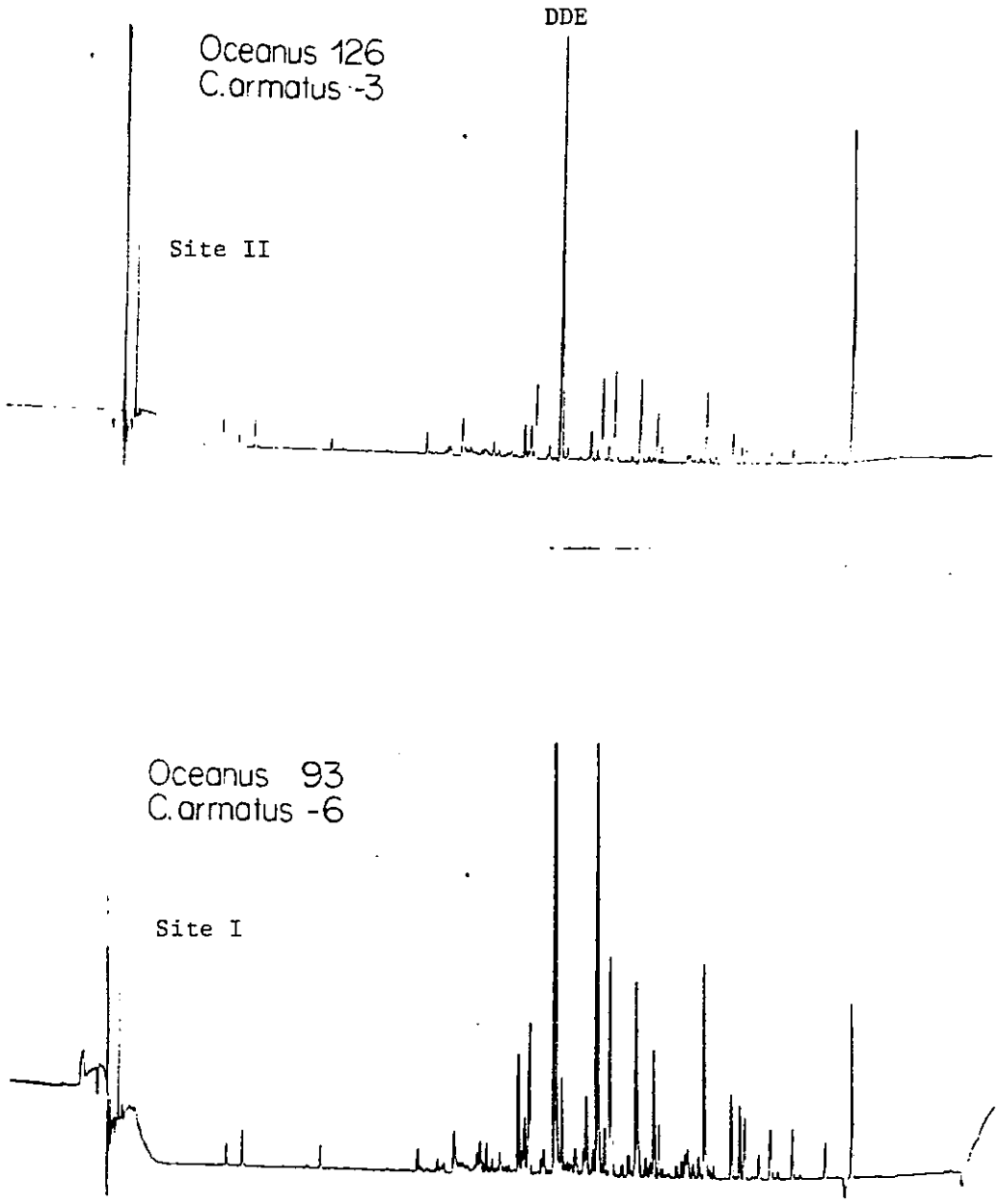


Figure 3.2.1 Capillary gas chromatograms (electron capture detector) of organochlorine pesticides and PCBs in livers of rat-tails (C. armatus).

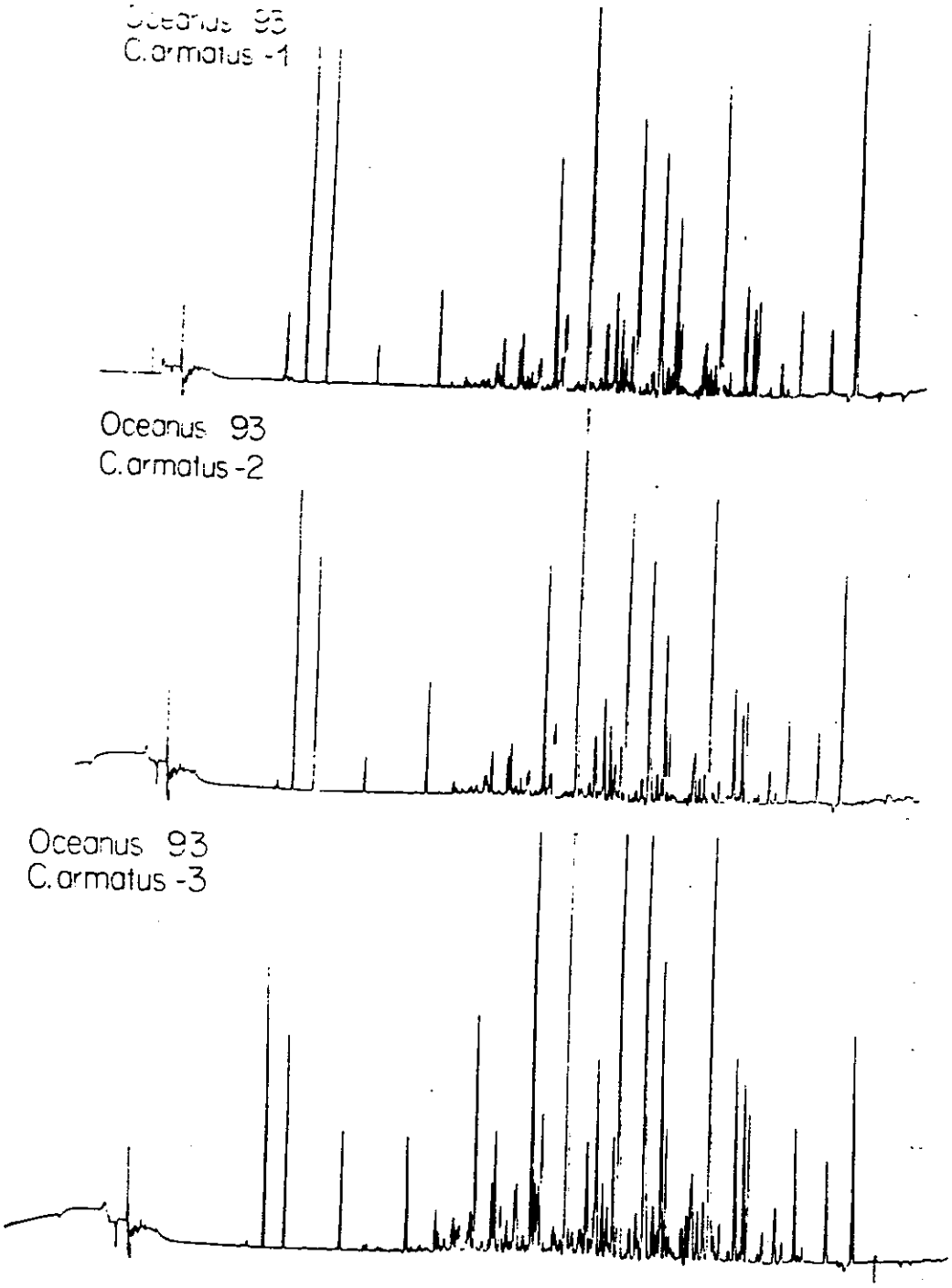


Figure 3.2.2 Capillary gas chromatograms (electron capture detector) of organochlorine pesticides and PCBs in livers of 3 individual rattails (C. armatus) caught at the same time at Site I.

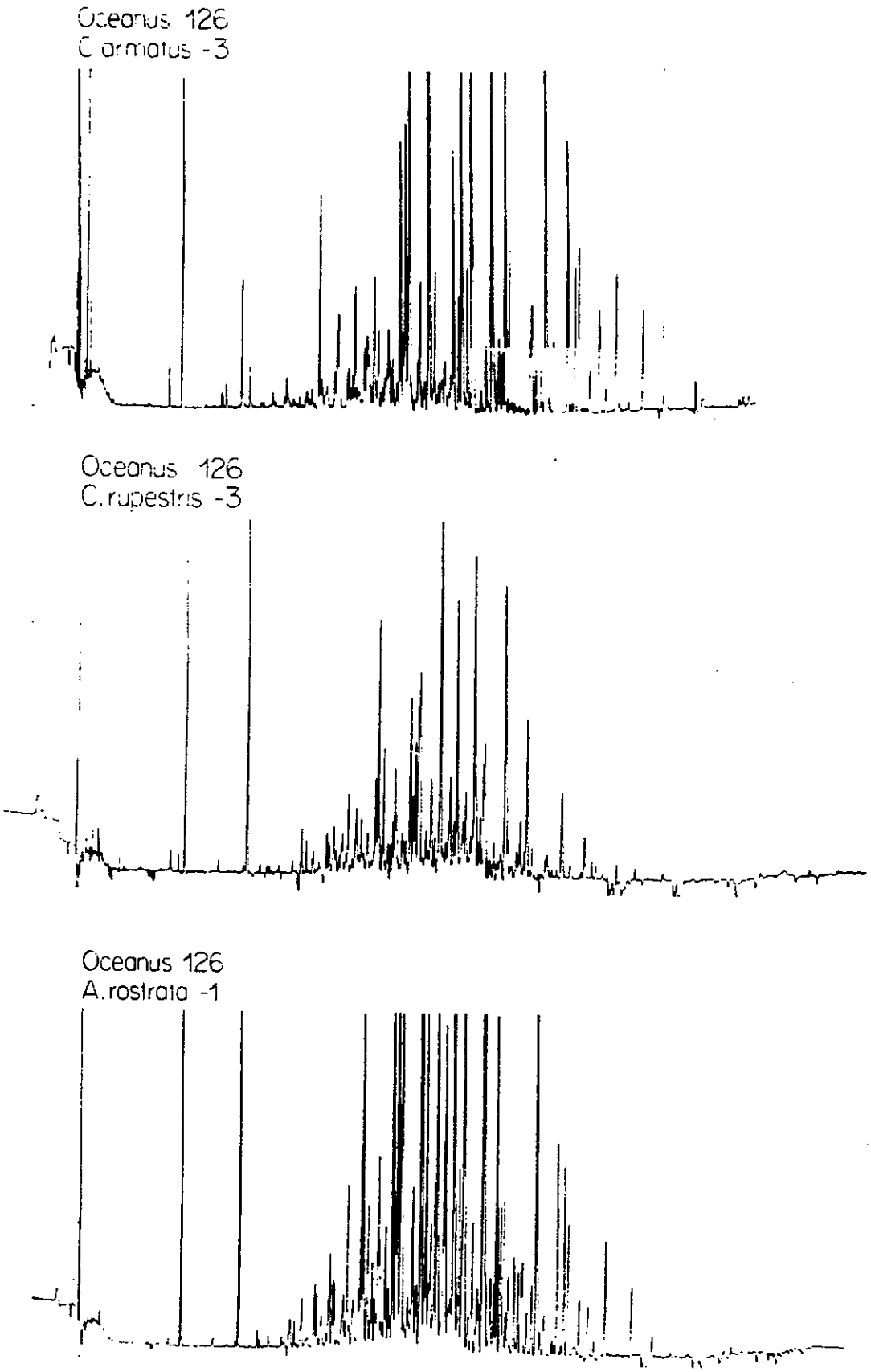


Figure 3.2.3 Capillary gas chromatograms (electron capture detector) of organochlorine pesticides and PCBs in livers of three species of rattails caught at Site II.

Figure 3.2.4

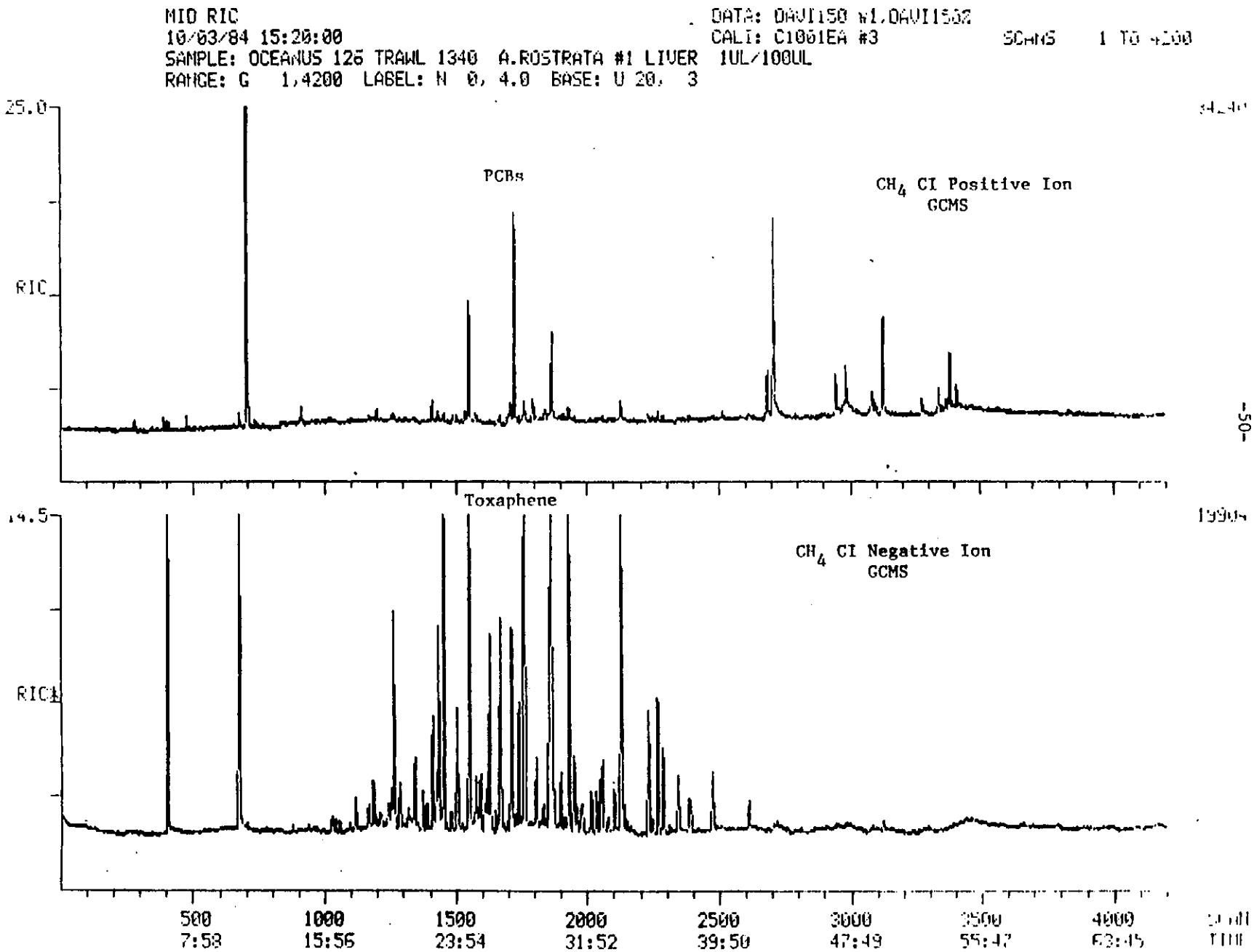

MID RIC
10/03/84 15:20:00
SAMPLE: OCEANUS 126 TRAWL 1340 A.ROSTRATA #1 LIVER
RANGE: G 1,4200 LABEL: N 0, 4.0 BASE: U 20, 3
DATA: DAVI150 #1,DAVI150
CALI: C1001EA #3
SCANS 1 TO 4200
1UL/100UL
25.0
RIC
PCBs
CH_4 CI Positive Ion
GCMS
Toxaphene
CH_4 CI Negative Ion
GCMS
RIC
500
7:58
1000
15:56
1500
23:54
2000
31:52
2500
39:50
3000
47:49
3500
55:47
4000

Figure 3.2.5

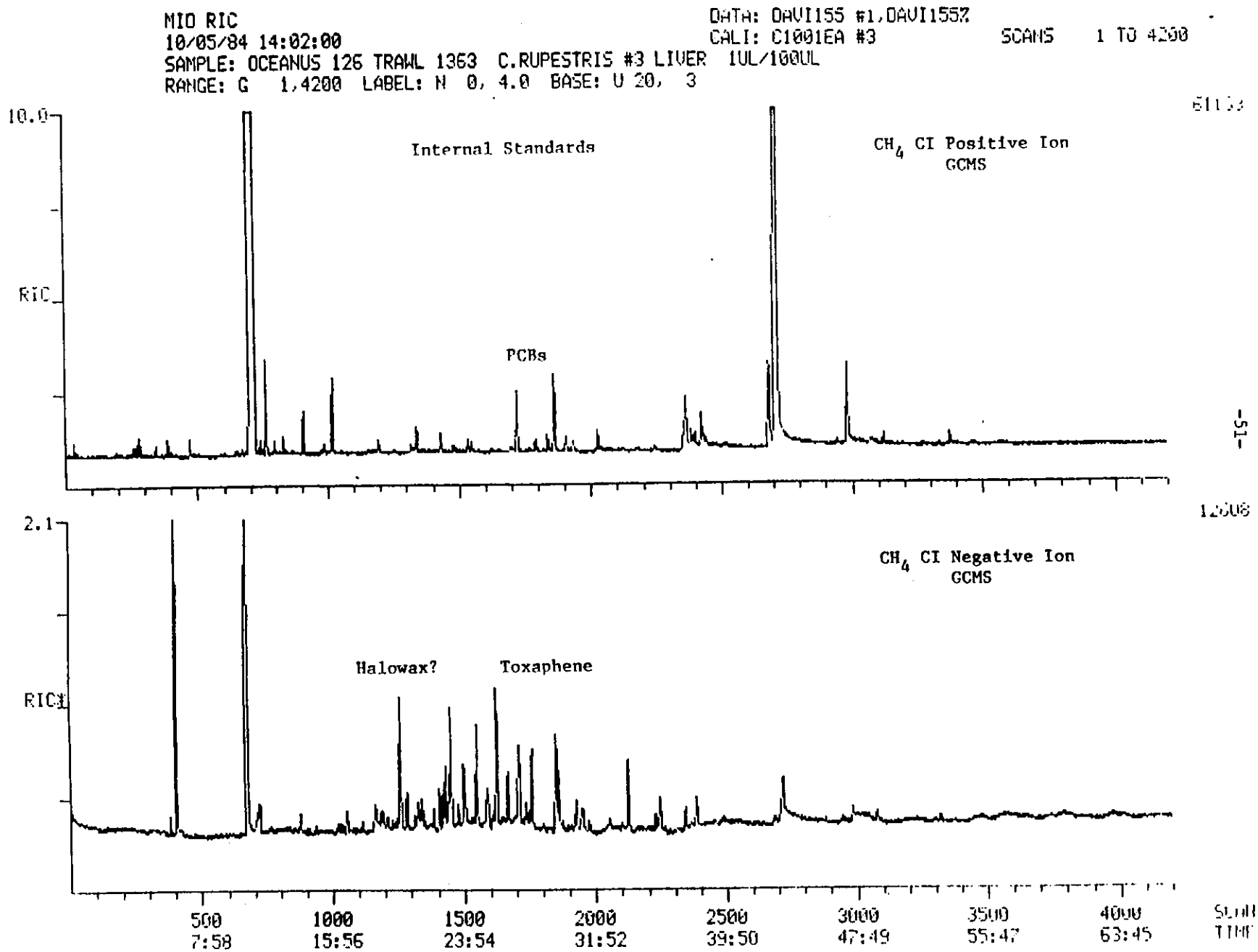

MID RIC
10/05/84 14:02:00
SAMPLE: OCEANUS 126 TRAWL 1363 C.RUPESTRIS #3 LIVER 1UL/100UL
RANGE: G 1,4200 LABEL: N 0, 4.0 BASE: U 20, 3
DATA: DAVI155 #1,DAVI155%
CALI: C1001EA #3
SCANS 1 TO 4200
10.0
RIC
Internal Standards
PCBs
CH4 CI Positive Ion GCMS
2.1
RIC
Halowax?
Toxaphene
CH4 CI Negative Ion GCMS
500 7:58
1000 15:56
1500 23:54
2000 31:52
2500 39:50
3000 47:49
3500 55:47
4000 63:45
SCAN TIME

Figure 3.2.6

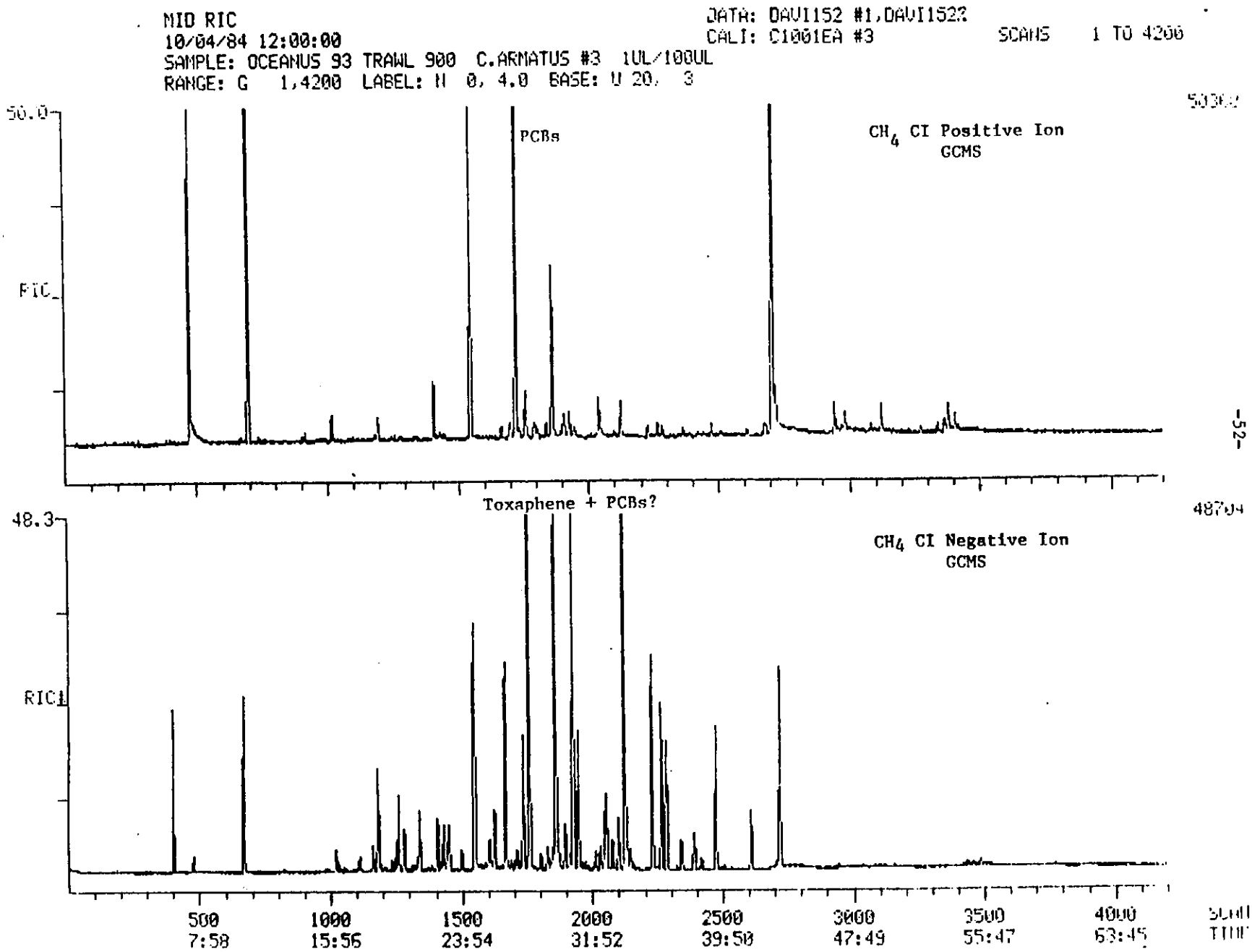
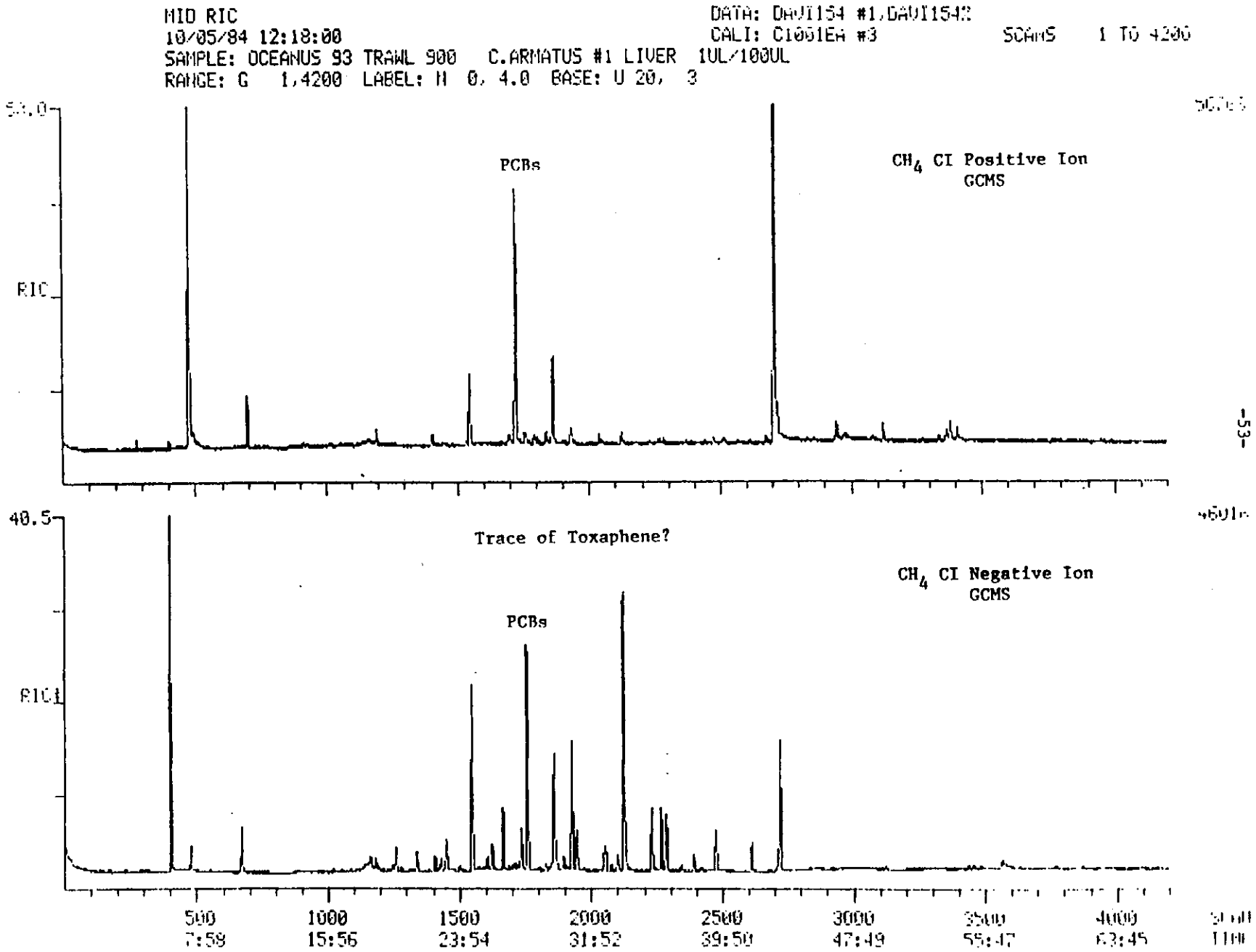

MID RIC
10/04/84 12:00:00
SAMPLE: OCEANUS 93 TRAWL 900 C.ARMATUS #3 1UL/100UL
RANGE: G 1,4200 LABEL: N 0, 4.0 BASE: U 20, 3
DATA: DAVI152 #1,DAVI152?
CALI: C1001EA #3
SCANS 1 TO 4200
50.0
RIC
PCBs
CH4 CI Positive Ion
GCMS
-52-
Toxaphene + PCBs?
48.3
RIC
CH4 CI Negative Ion
GCMS
500
7:58
1000
15:56
1500
23:54
2000
31:52
2500
39:50
3000
47:49
3500
55:47
4000
63:45

Figure 3.2.7


MID RIC
10/05/84 12:18:00
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RANGE: G 1,4200 LABEL: H 0, 4.0 BASE: U 20, 3
DATA: DAVI154 #1,DAVI154#
CALI: C1001EA #3
SCANS 1 TO 4200
RIC
PCBs
CH4 CI Positive Ion
GCMS
Trace of Toxaphene?
CH4 CI Negative Ion
GCMS
500
7:58
1000
15:56
1500
23:54
2000
31:52
2500
39:50
3000
47:49
3500
55:47
4000
63:45

Figure 3.2.8 Toxaphene Standard

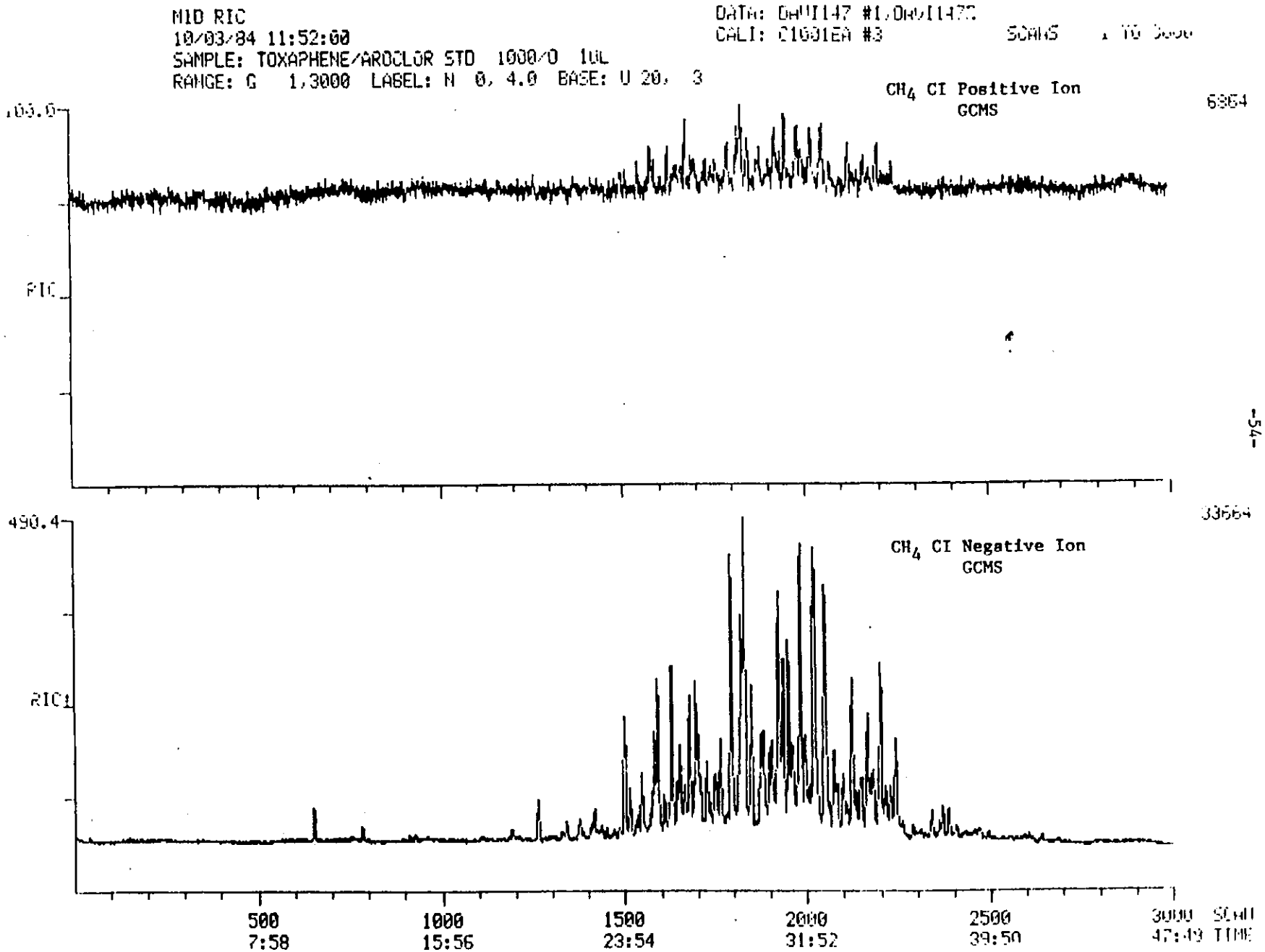
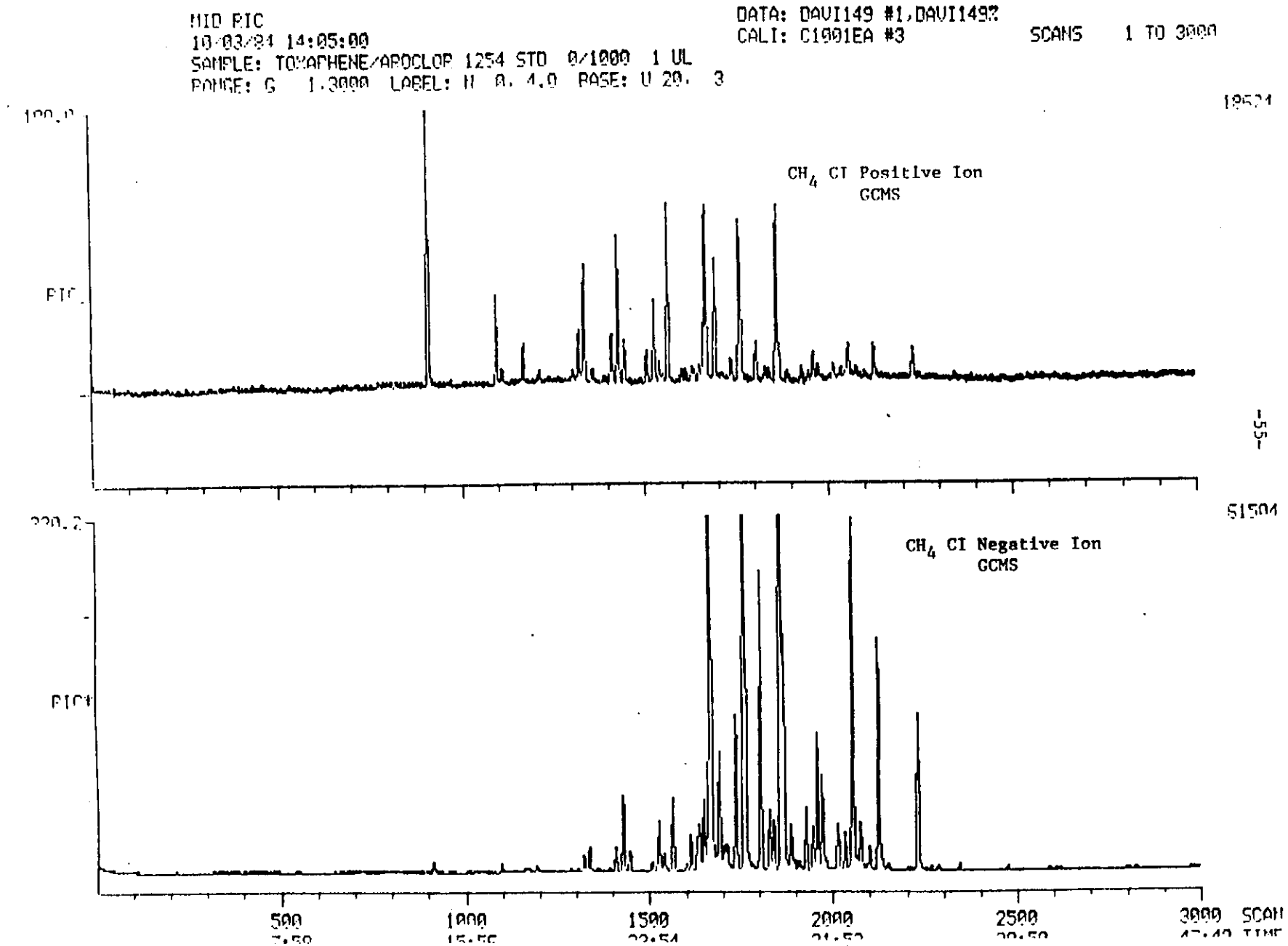


Figure 3.2.9 PCB Standard



III. 3. Trace Metals

The majority of body burden data for trace metals in marine organisms in the literature since 1970 are for mercury; presumably because of the human health concern over high concentrations of mercury in swordfish and tunafish (Ryther and Officer, 1981). Weiss et al. (1971), based on estimates of the mercury geochemical cycle and ice core measurements from Greenland, reason that man's activities would add only about 15% to the mercury burden to the upper ocean and less (by our reference) to the deeper ocean water. Matsunaga (1981) has corrected the earlier geochemical cycle estimates (e.g. those of Weiss et al., 1971) using more recent and more accurate mercury data for seawater. However, the original conclusion that man's activities will not cause widespread increases in mercury concentration in marine organisms remains valid. This does not rule out the obvious local effects demonstrated by the case for Minamata Bay (Ryther and Officer, 1981).

Data for mercury provides an example of the extent of our knowledge of chemical body burdens of environmental concern in organisms of the open ocean. For this reason, a brief discussion of available literature is instructive to the overall purpose of this report. Only a few data relate directly to deep ocean organisms living below 1000 meters. Barber et al. (1972) report mercury in several species of bottom dwelling fish from 2500 meters caught in 1971 and 1972 off the east coast of the U.S. at 34°45.3'N, 75°11.8'W and 34°18.2'N,, 75°32.6'W. Table 3.3.1 is reproduced from their paper. These authors had also analyzed two museum specimens and these data are also presented in Table 3.3.1.

Barber et al. suggest that differences in concentrations of mercury between A. macrochir when compared to the Chalinura and Anitmora result from species specific metabolic processes as all three species appear to be similar in feeding behavior. A correlation was found between length of fish and mercury concentrations for the A. rostrata, the only species where a range of sizes permitted such a comparison. Museum specimens contained similar concentrations of Hg as did the more recent fresh samples (Table 3.3.1) indicating that anthropogenic activities caused no detectable influence on Hg concentrations found in bathypelagic fish.

Cross et al. (1973) reported on Mn, Fe, Cu, Zn in the A. rostrata from this same sample set and concluded that the concentrations of these trace metals showed no significant correlation with size of fish in contrast to the findings for mercury. They suggested that the four transition metals were more actively bioregulated by the fish while mercury was less so because of biochemical properties of both inorganic and organic mercury species.

In regard to the comparison of museum samples with present day samples, Gibbs et al. (1974) point to sampling problems due to different preservatives, label tags included in jars, and species differences; all of which diminish the value of using museum specimens to establish trace metal body burdens at time of capture. They conclude "Until the effects of preservation are properly understood, fluid preserved museum specimens cannot be used for meaningful comparisons of metal concentrations either with other museum specimens or with frozen specimens." Miller et al. (1972), however, present data demonstrating it is unlikely that the museum specimens they analyzed were contaminated to a significant extent by preservation. Very low concentrations of Hg (0.17 $\pm$

0.15 ppm dry weight) were detected in a pipefish specimen preserved in the same manner as the swordfish samples.

Most of the data available for trace metal body burdens in open ocean organisms relates primarily to mercury in large, predatory upper open ocean fish such as tuna and swordfish. Figure 3.3.1, taken from Barber and Whaling (1983) summarizes a large data set collected from various published reports. This data illustrates the relationship between body size and Hg concentration in three species, blue marlin (Makaira nigricans), white marlin (Tetrapterus albidus), sailfish (Istiophorus platypterus). The relationship shown is for female fish but a similar correlation is found for a composite grouping of male and female fish. This study is of special significance because of the large size of the data set and because the authors give data for intercalibration. Several authors have reported concentrations of mercury in tunafish, swordfish, sharks and marlin (Menasveta and Scriyong, 1977; Rivers et al., 1972; Shultz and Crear, 1976; Shultz et al., 1976; Shultz, 1979; Miller et al., 1972; Takeda et al., 1976; Kai et al., 1983; Freeman and Horne, 1973; Mackay et al., 1975; Ahmed et al., 1981; Powell et al., 1981; Bousch and Thielke, 1983a,b). As found by Barber and Whaling (1983), there was usually some relationship established between mercury concentration and some measure of size such as length or body weight. Correlation equations were often different for different species however, even if the organisms were caught in the same general area of ocean. Freeman and Horne (1973) established the important fact that small subsamples of edible muscle of the swordfish were representative of whole muscle tissue as far as total mercury concentration is concerned.

Selenium has been measured in a few of the same samples analyzed for mercury (Mackay et al., 1975; Kai et al., 1983; Takeda et al., 1976). A positive

correlation was noted between Hg and Se concentrations (Mackay et al., 1975) but in other cases inverse correlations were found depending on the type of tissue analyzed (Kai et al., 1983). Koeman et al. (1973) report selenium-mercury correlations in seals and present a brief discussion of the biochemistry of selenium and mercury in marine fish and mammals.

The literature on marine mammals was not exhaustively searched for this project but several papers were acquired that bore some relation to the open ocean or to physiological changes. Marine mammals have been analyzed for mercury concentrations in several studies because of the concern for their health and as representative top of food chain predators that might give clues to potential human exposure. Gaskin et al. (1972; 1979) report on changes in mercury levels in harbor porpoises from the Bay of Fundy and adjacent waters during 1969-1977. Gaskin et al. analyzed several different tissue types from both male and female porpoises. As with the studies previously cited for large predaceous fish (tuna, swordfish, marlin), there was a relationship between age (size ?) and increasing mercury concentration. Mercury in muscle tissue was almost all in methylated form, while an average of 17% of the mercury in liver was methylated. There were significant temporal changes in the mercury content over the 1969-1977 period with a decrease from 1970 to 1971 remaining lower until 1974 when there began a steady increase. The authors discounted changes in diet and nutrition and speculate that these changes might be associated with intrusions of relatively mercury-poor Gulf Stream water in the Bay of Fundy as compared to the usual dominance of waters of the Nova Scotia current. This conclusion is tentatively supported by temperature records.

Falconer et al. (1983) report on mercury, cadmium, copper and zinc concentrations of porpoises (Phocoena phocoena) from United Kingdom coastal waters. Mercury and cadmium levels tended to increase in liver and kidneys with increasing length of animal. The proportion of methylmercury (9-57%) in liver decreased with increasing total mercury. The data suggest that mercury and cadmium concentrations are influenced to a lesser extent by biological-physiological controls in the animal than are copper and zinc.

The distribution of mercury between different tissues from animals on the Canadian and U.K. coasts were similar with some of the larger porpoises from the Canadian coast showing higher mercury concentrations. Falconer et al. (1983) also point out that the large variance in mercury and cadmium concentrations obtained from porpoises in part of the North Sea imply a limited usefulness of this species as indicators of environmental quality.

Honda and co-workers (Honda et al., 1982; Honda and Tatsukawa, 1983) report data for cadmium, zinc, iron, copper, manganese, lead and nickel in striped dolphins (Stenella coeruleoalba) in the Northwest Pacific. Kidneys showed highest cadmium concentrations, but the hepatopancreas concentrations were also high. A positive correlation between zinc and cadmium in kidney and liver was also reported. Organ specific age trends were found and cadmium and zinc showed rapid changes related to reproduction and weaning in females and pups.

Windom et al. (1973) report mercury concentrations in several samples of North Atlantic upper ocean plankton (Figure 3.3.2). Based on this and other data, they suggest that the concentration of Hg in plankton tends to decrease with increasing distance from sources of pollution in North America. "In all

areas studied, the open ocean 'unpolluted' plankton populations generally have concentrations ranging from less than 0.1 to about 0.4 ppm. This contrasts to the nearshore, potentially polluted plankton populations which have mercury concentrations ranging from less than 0.2 to 1.0 ppm or more." Windom et al. (1973) also reported that the concentrations of Hg may be independent of the biological composition of the sample. In another study, Windom et al. (1973) report on concentrations of arsenic, cadmium, copper, mercury and zinc in some species of North Atlantic finfish collected in the Sargasso Sea east of the Gulf Stream and inshore off the southeastern U.S. coast. They analyzed 91 individuals representing 35 species of finfish (Chondrichthys and Osteichthys). Results indicate that the metal concentrations were similar for both inshore and offshore species, with Chondrichthys showing higher concentrations compared to Ostreichthys. All other metal concentrations were similar between the two groups. Metals were consistently higher in concentration in livers of Chondrichthys except for mercury which was present in higher concentrations in muscles.

Williams and Weiss (1973) measured mercury in several components of the pelagic food chain 450 km southeast of San Diego, CA. They reported that "mercury content in almost all of the higher trophic levels of organisms collected at greater depths (> 500 m) was indistinguishable from the concentration of mercury in zooplankton at these depths." Leatherland et al. (1973), measured concentrations of zinc, arsenic, cadmium, antimony and mercury in pelagic organisms, mainly crustacea and fishes collected off northwest Africa and in the Azores region, and reached the same conclusion as Williams and Weiss (1973): i.e. "Concentrations of mercury (0.06 to 0.38 ppm dry weight) showed no clear trend with trophic level."

Gilmartin and Revelante (1975) report that the northern Adriatic anchovy Engraulis enrasicholus contained Hg ranging from 75 to 215 x 10^{-9} g/g wet weight tissue and were 2-4 times greater than in the same or similar anchovy species off northwestern Africa, southeastern U.S. and California. These workers also analyzed for copper, nickel, lead, silver, and cadmium in the same species and compared data on all these metals, including mercury, with data for the sardine (Sardinia pilchardus) caught in the same area. Both mercury and copper showed interspecific differences, while the other metals did not. Mercury concentrations were higher in anchovy muscle tissues compared to sardines in contrast to an earlier report (Establier, 1972) of no concentration differences for species caught off northwest Africa.

Boyle (1981) reports data for Cd (cadmium), Zn (zinc), Cu (copper) and Ba (barium) in foraminifera tests. The intent of his work was to establish relationships between contemporary seawater concentrations of these metals and concentrations in forams to establish a basis for using metal concentrations in foram tests as a paleoecology-paleoceanic circulation investigative tool. Results for Cd and Zn were very good but residuals contamination for Cu and Ba created an analytical problem. In principal, this approach could be used to monitor changes in metal concentrations in benthic communities where foraminifera are present. At the other extreme of the water column, the neuston or "pleuston", Schulz-Baldes and Cheng (1980) report a very interesting data set for Cd in Halobates micans. This marine insect, commonly called the sea-skater, lives at the sea surface. They analyzed 428 samples from 57 locations and compared their data with other data as indicated in Table 3.3.2. Differences in observed concentration are mainly related to biological processes

which may control the biogeochemical cycle of Cd but further investigation is required before assigning causative control mechanisms. Schulz-Baldes and Cheng make the suggestion that these organisms may effectively serve as a sentinel organism of the open ocean for metal contamination in much the same manner as bivalve molluscs are employed in coastal water; a suggestion worthy of serious consideration.

The Mediterranean has often been referred to as a polluted sea. Bernhard (1978) reviewed data concerned with heavy metals and chlorinated hydrocarbons in the Mediterranean. His review shows that in 1978 there were very few data on organisms of the meso, bathypelagic and deep water benthos, a situation which apparently has not improved in the intervening years.

Ray (1984) has provided an up-to-date, useful, succinct review of the bioaccumulation of cadmium in marine organisms. An important point to be made in this regard is extrapolation. Knowledge of coastal and estuarine organism trace metal biochemistries will be complicated by salinity influences and the role of suspended matter. Both salinity and suspended matter type and concentrations are significantly different when comparing coastal and deeper open ocean waters.

It is difficult to improve on the succinct summary and concluding statement of Ray (1984) which applies in general to most trace metals:

"It has been established that, although Cd occurs in the marine environment in only trace concentrations, most marine organisms, especially molluscs and crustaceans, can accumulate it rapidly. Cadmium is not uniformly distributed in the body and selectively accumulates in specific organs like liver, kidney, gills, and exoskeleton. The concentrations in muscle tissues are

several orders of magnitude lower. The disposition of Cd in the organisms in the laboratory studies generally parallels those in nature.

A number of biotic factors like body size, maturity, sex, etc. influence bioaccumulation but extensive studies are still lacking.

The chemical form of Cd in the environment is of prime importance in bioaccumulation by marine organisms. Salinity can affect the speciation of Cd, and bioaccumulation is affected by both temperature and salinity. The ultimate level of Cd in the organisms will depend not only on the biotic and abiotic factors but also on metabolism of the metal by the organisms. A few studies indicate depuration of Cd by some bivalves but other organisms show very effective retention of Cd. Metallothionein formation for detoxification and storage has been observed in a large variety of marine organisms. Recent reports indicate an alternate storage and excretion mechanism in the formation of membrane-limited vesicles or granules. There seems to be a common link between intracellular localization of Cd in metal-binding proteins and Cd containing vesicles as detoxifying mechanisms in the marine organisms.

Much of what is known about Cd bioaccumulation by marine organisms has come from laboratory studies and there are inherent dangers in trying to extrapolate the results to field situations. In spite of tremendous progress made over the years, the basic understanding of the bioaccumulation process is still very nebulous and will remain so until the uptake, storage, and elimination processes are fully understood."

There are numerous references to analysis of metals in birds and feathers of birds which we have not cited as they are beyond the scope of this review. Most deal with coastal feeding birds or Arctic or Antarctic species. Witkowski

and Frazier (1982) briefly review the scant data on metals in sea turtles which essentially highlights the lack of data and knowledge on this subject.

Thus, we have found data on heavy metals in several of the species of top of food chain predatory mammals and large fish. The available data is primarily on mercury, with a small amount on cadmium and very little on other metals. The data for other species of the open ocean foodweb are very scarce or at least difficult to find in searching the literature.

Table 3.3.1 (from Barber et al., 1972)

Mercury concentrations in the axial muscle of benthopelagic fish. The values given are the means of three to six replicates, ± 1 standard deviation. The recent fish were caught on 28 July 1971 and 5 July 1972.

Species	Length (cm)	Hg (ppm, wet weight) DUML***	AEFC***
		Recent fish	
Aldrovandia macrochir	54.5	0.07 ± 0.01	0.09 ± 0.04
	55.0	0.3 ± .02	
	58.0	.04 ± .016	.04 ± .009
	66.0	.04 ± .009	.02 ± .004
	67.5	.08 ± .007	.09 ± .018
Antimora rostrata	32.3	.32 ± .01	.30 ± .02
	33.4	.43 ± .02	.45 ± .02
	33.5	.24 ± .02	.26 ± .05
	35.5	.31 ± .04	.40 ± .04
	39.0	.53 ± .04	
	42.8	.58 ± .02	.59 ± .04
	45.3	.65 ± .06	
	45.8	.71 ± .004	.71 ± .09
	52.2	.76 ± .02	.74 ± .02
Bathysaurus agassizi	42.4	.36 ± .07	
Chalinura brevibarbis	28.8	.38 ± .03	
	39.1	.42 ± .02	.45 ± .01
Chalinura carapina	27.5	.36 ± .02	
		Old Fish	
Antimora rostrata*	45.7	0.50 ± 0.03	
Aldrovandia macrochir**	43.5	.11 ± .02	

*Collected 1 August 1883.

**Collected 24 October 1886.

***DUML - Duke University Marine Laboratory
AEFC - Atlantic Estuarine Fisheries Center, NMFS, NOAA, U.S. Dept. of Commerce

Table 3.3.2 (from Schulz-Baldes and Cheng, 1980).

Literature values for cadmium concentrations of *Halobates* from various locations.

Species	Location	µg Cd g^{-1} d.w.	Author
H. sobrinus	Gulf of California	99.0 - 208.0	Cheng et al., 1976
H. sericeus	Hawaii	40.0	Cheng et al., 1976
H. micans	Tropical Atlantic Ocean	1.0 - 309.0	Bull et al., 1977
H. micans	Tropical Atlantic Ocean	1.7 - 122.0	This paper
H. robustus	Galapagos Islands	6.0 - 8.0	Cheng et al., 1979
H. flaviventris	Palau Islands	1.4 - 6.9	Schulz-Baldes and Cheng (unpublished data)
H. nereis	Palau Islands	1.2 - 2.7	Schulz-Baldes and Cheng (unpublished data)
H. mariannarum	Guam, Truk Island	0.9 - 6.2	Schulz-Baldes and Cheng (unpublished data)

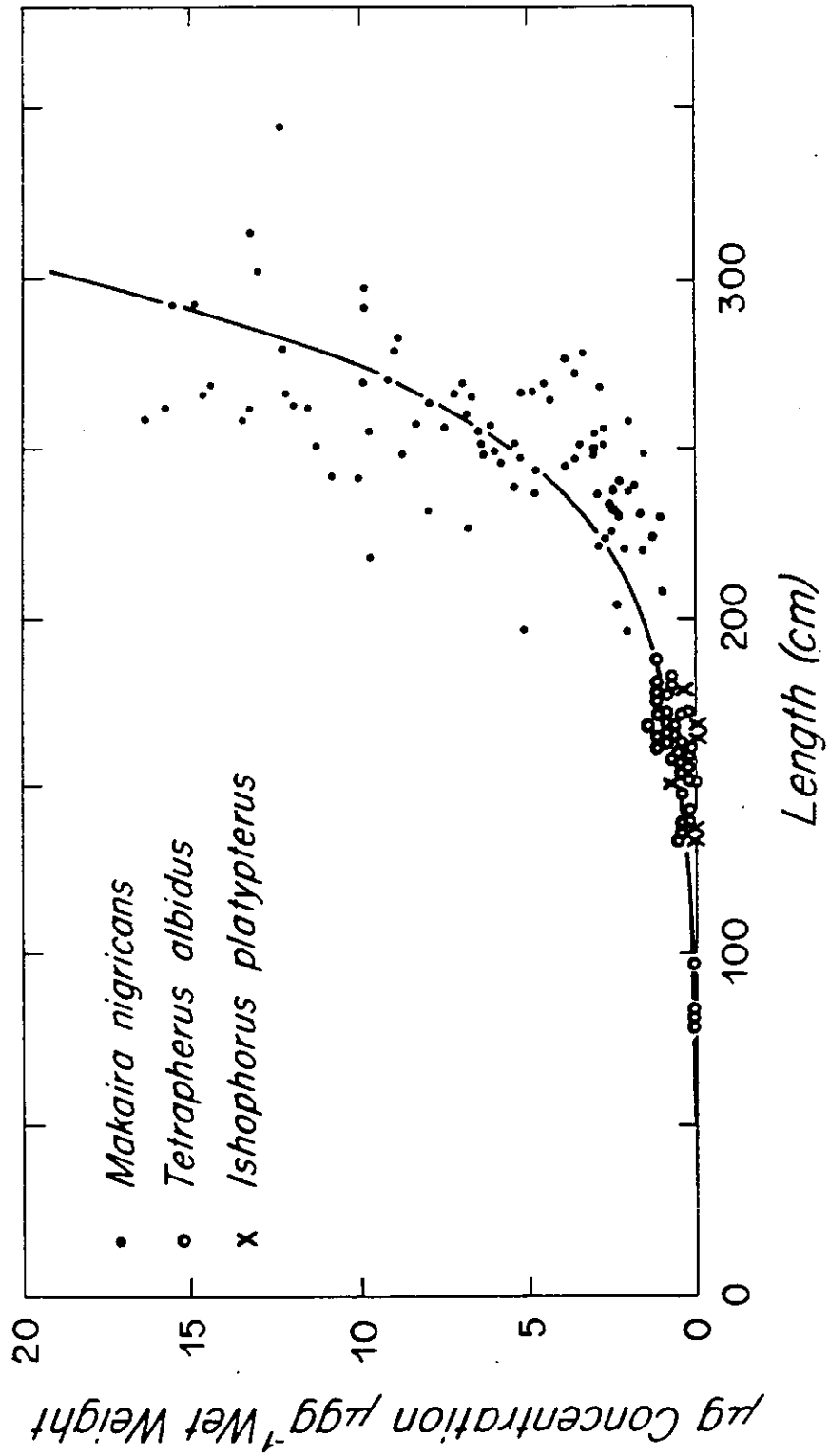


Figure 3.3.1 From Barber and Whaling, 1983 (Figure 1).

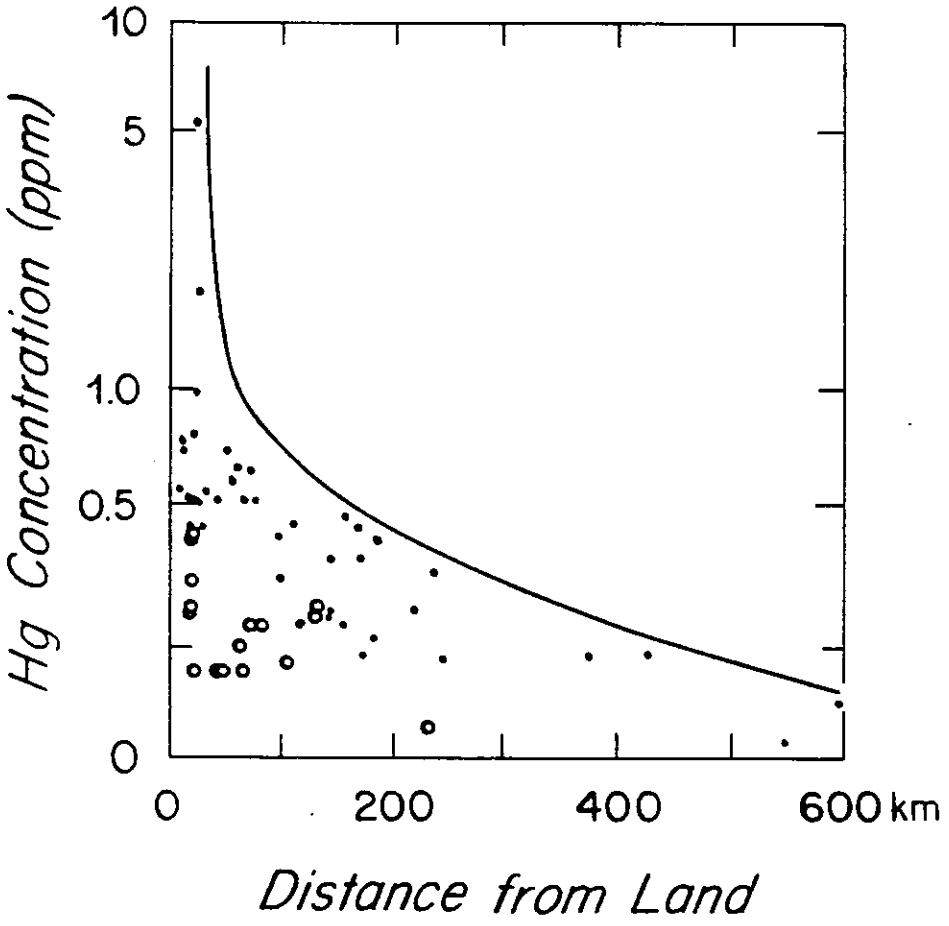


Figure 3.3.2 From Windom et al., 1973 (Figure 4).

III. 4. Discussion of Coastal/Continental Shelf Data and the Relation to Biogeochemical Cycles in the Deep Sea and Body Burdens of Open Ocean Organisms

The extent to which we can extrapolate from body burden data of coastal/continental shelf organisms to deep ocean organisms obviously depends on the degree of certainty that we wish to assign to the extrapolation. We can state that all the factors assigned by Ray (1984) (quoted in Section III. 3.) to the controls of Cd body burdens generally applies to other contaminants in all marine organisms. Phillips (1980) in his book on quantitative biological indicators has admirably reviewed issues of age, size, lipid content, metabolism, reproduction, feeding strategies, conditions of exposure as they relate to chemical contaminants in coastal marine biota. The relative importance of each of these factors to the deep ocean biota is not understood to any appreciable extent except for lipid content which is of clear importance for lipophilic compounds (e.g. organochlorine pesticides and PCBs).

It appears that food web magnification is not an important process for most coastal and surface water species except perhaps for large predator fish, birds, and mammals. The same seems likely to apply for deep ocean species with the caveat that differing feeding strategies may be a greater influence in deep ocean biota.

A major problem in assessing the known and predicting the potential body burdens of deep ocean biota relates to the complex interactions between physical, biological and geochemical processes in delivering a biologically available pollutant to the deep ocean. Numerous references included in our biblio-

graphy document the importance of atmospheric transport to the deep ocean for contaminants such as the organochlorine pesticides and PCBs. However, Harvey and Steinhauer (1976) and more recently Tanable and Tatsukawa (1983) have noted that the various compounds probably have differing rates and pathways of movement once they enter the system due to differing physical-chemical forms in the atmosphere and differing solubilities and solid/solution partitioning in the water. In addition, chemicals measured as parent compounds make up a small fraction of the total contaminant burden including metabolites (Gosset et al., 1983, 1984) and analyses of oxidation products (e.g. metabolites) is an important aspect of any assessment.

Figure 3.4.1 presents a schematic of physical processes acting on the wastes entering the oceans. Figure 3.4.2 presents our assessment of the state of knowledge as to what happens to contaminant chemicals in meso- and bathypelagic zones. The influence of meso- and bathypelagic biota on the physical-chemical form of compounds such as PCBs, Toxaphene, DDE and PAH are largely unknown. Our knowledge of meso and bathypelagic biology is only now being extended in a quantitative sense to the fragile life forms not previously caught in recognizable forms in nets (e.g. Harbison, 1985). These organisms could have a very important role in controlling rates and pathways indicated in Figure 3.4.2 and as such control the physical-chemical form of contaminant exposure for deep ocean communities.

Another important point to consider is that there are no generally accepted data for concentrations of fossil fuel compounds and organochlorine compounds in meso- and bathypelagic waters. Even the data of Tanabe and Tatsukawa (1983) contains cautionary statements about sampling contamination problems. The

data sets for fossil fuel compounds and organochlorine compounds in surface sediments are meagre and collected over five years ago during the early development stage of high resolution GC and GCMS analyses. In regard to the analyses of water, technology has progressed to the point where this previously very difficult analysis is now feasible with some additional effort for adaptation to the high pressure conditions of the deep ocean (de Lappe et al., 1983).

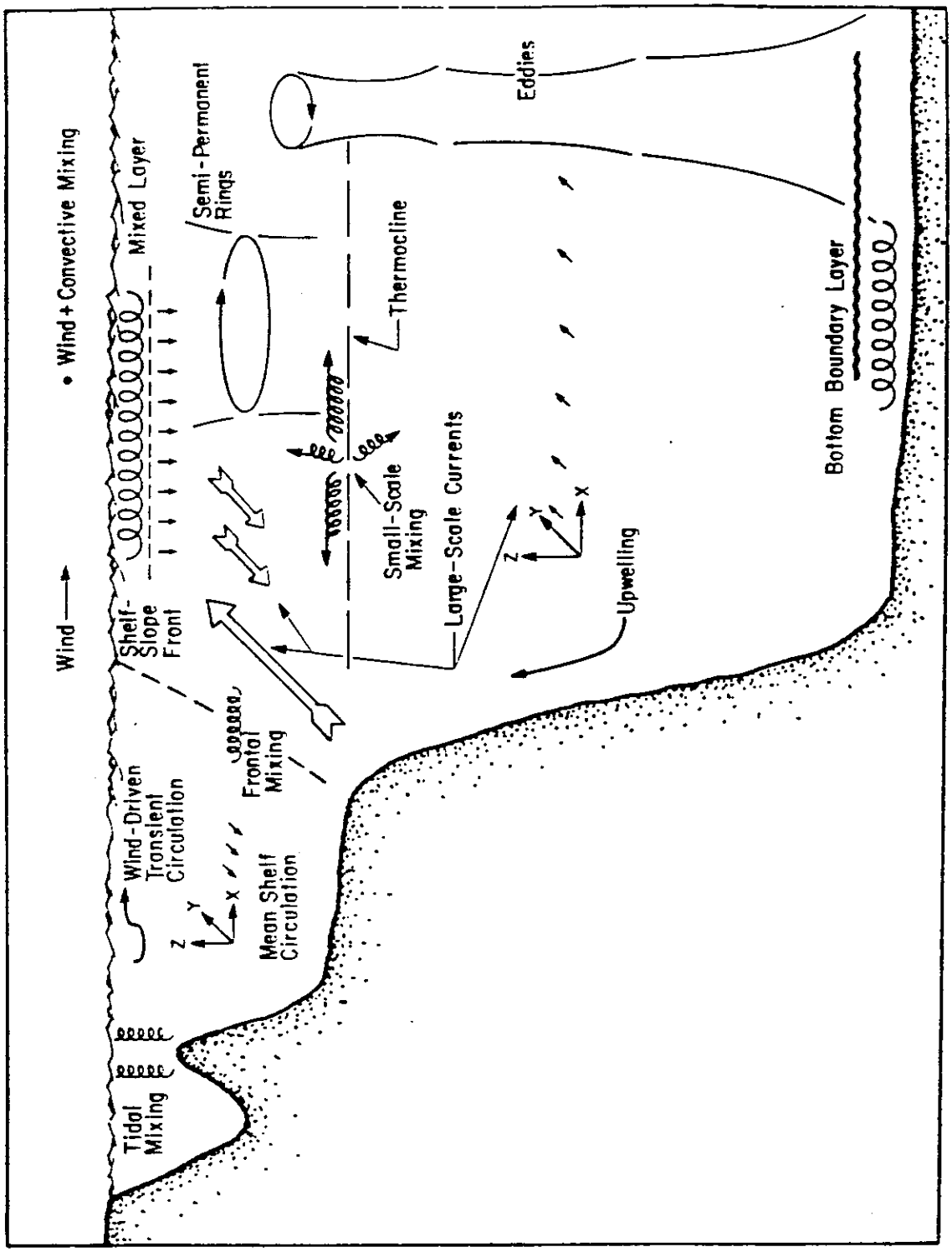
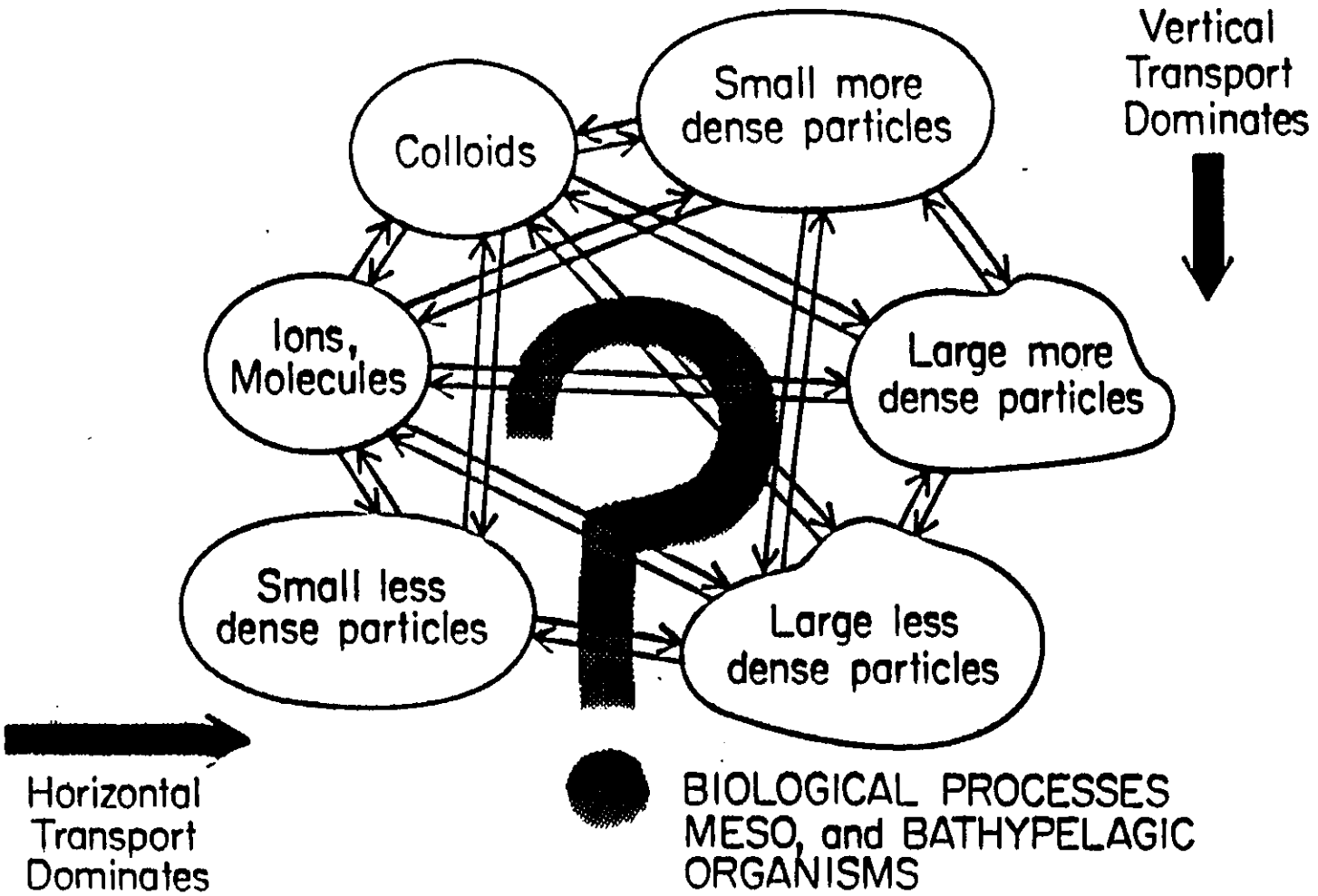


Figure 3.4.1 Physical processes acting on waste disposal in the ocean.

Figure 3.4.2

CONCEPTUAL MODEL



III. 5. Summary of Body Burden Data and Recommendations for Research

Summary

1. The body burden data for trace metals and organic pollutants in deep sea biota are very limited. Of the available data, most are for mercury, DDT and PCBs and of the DDT and PCB data almost all are for rattail livers. Most of these data are for samples obtained on the continental slope off the eastern coast of North America.

2. The available data show that PCBs and DDT have penetrated to the deep ocean in forms that are available for uptake by biota. Penetration to the deep ocean occurred much more rapidly than was originally predicted.

3. There is no evidence of elevations of trace metals in deep sea biota as a result of man's activities.

4. Concentrations of PCBs and DDT in deep sea fish livers approach levels which some workers suggest might have long term deleterious effects. This prediction is based on very limited data for fresh water and coastal species.

5. The literature relating body burdens of any organic contaminant in aquatic species to a specific measured adverse effect were not reviewed here but are also meagre. Most experiments involve assessment of concentrations in the exposure habitat and observed effects in the organism; or concentrations in the habitat and uptake and metabolism by the biota but not effects. Rarely have body burden and effects data been systematically collected.

6) Measurements of body burdens of PCBs, DDT, polynuclear aromatic hydrocarbons and presumably many other organic contaminants in organisms other than bivalves can be severely misleading because metabolism of the compounds can

mask the true exposure history. Evidence from a few coastal studies clearly indicate that much of the PAH, DDT, and PCB body burden could be in the form of oxygenated metabolites not easily measured by current methodology.

7) The relationship between exposure, physical-chemical form, uptake of a pollutant, metabolism, excretion or release across membrane surfaces for organic chemical contaminants in coastal and continental shelf organisms provides a general guide to thinking about similar processes in deep sea biota. However, the role of factors such as exposure from sediments, differing life histories and feeding strategies and other factors (see Grassle section this report) indicate that extreme caution must be used when extrapolating from coastal studies to the deep ocean. For example, if organismal biochemistry of deep ocean animals is different because of evolutionary adaptation to combined pressure and low temperatures of the deep ocean, then membrane transfer and lipid composition, both important factors in governing body burdens, may function quite differently compared to shallow water organisms.

8) Our new data for organochlorines in deep ocean rattail livers show contamination by PCBs, DDE, and Toxaphene with possible indications of Halowax (polychloronaphthalene) contamination. High resolution glass capillary gas chromatography and GC/MS data suggest that at least the PCBs have been subjected to metabolism. The distribution of PCBs is similar to that found in coastal organisms, marine mammals and birds.

There appears to be a higher amount of Toxaphene relative to PCBs in fish livers caught on the slope off Nova Scotia compared to those caught on the slope near the Hudson Canyon. No reason for this discrepancy is offered at this time.

9) The data for PCBs, DDT, and petroleum hydrocarbons in pelagic open ocean communities indicate no evidence of food web magnification. Except for large predatory fish such as tuna, mammals and birds there appears to be no biomagnification through the food chain. This is apparently due to the ability of organisms to utilize metabolic processes and exchange across membrane surfaces to control body burdens. The elevated concentrations found in some large, long-lived species has been related to age rather than location in a food chain.

10) Data for organochlorine compounds, fossil fuel compounds, and other organic pollutants in open ocean water are also rare because of sampling contamination problems compounded by the need for extremely low detection limits. Similar data for surface sediments are also meagre and date mostly to the mid-1970's when analytical methods of lower resolution were in use. The available data for water suggest the organochlorine compounds are behaving in a manner generally consistent with their solubilities and vapor pressures.

11) Biogeochemical cycle models which could be used to calculate expected exposure levels, and thus body burdens, under a variety of ocean dumping scenarios are imprecise because of a lack of: a) good knowledge of meso- and bathypelagic biology/food webs; b) good seawater solubility data for many of the compounds of concern; c) field verification in even a few cases for deep ocean systems.

Recommendations

1) There is a need for a larger data set for body burdens of organic chemical contaminants in a wider range of species, especially those with different feeding strategies. An assessment of lipid biochemistry should be included in this research.

2) In order to provide reasonable predictive models of exposure levels for deep ocean communities, there is a need to better understand the entire biogeochemical cycle in the water column and surface sediments. Specific areas where significant advancement can be made include:

i) dissolved, particulate matter concentrations;

ii) analysis of surface sediments including solid phase and solution interactions (interstitial waters);

iii) basic studies of meso- and bathypelagic biology.

3) For both shallow water and deep water, there is a need to better understand the relationship between chemical measurements in water, sediment, particulate matter and bioavailability.

4) To better understand the fate of organic contaminants in biota, analysis must include oxygenated reaction products as well as parent compounds.

Supplemental Text References

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III. 6. Bibliography

Body Burdens in Deep Ocean Communities

Published literature concerning contaminants in open ocean organisms has been sought both manually and with computer assistance. Manual search is extremely time consuming, even when one is already familiar with the subject and the likely publication sources. Manual searching was therefore confined to three areas: 1) published compilations, i.e. Marine Pollution Research Titles and Deep Sea Research Oceanographic Literature Review, 2) contact with colleagues, internationally, and 3) personal reprint collections and previous experience. After reviewing several computer compilations we chose to use Biological Abstracts and Aquatic Science and Fisheries Abstracts because these contain the best oceanographic and international collections. We found it difficult to selectively search for open ocean literature as it is not filed in that manner; we therefore searched indirectly by deleting subject areas in order to reduce an initially massive data file. We deleted from consideration the following:

coastal, including estuaries, harbors, etc.

toxicity and sublethal effects

coastal species, i.e. mussels, mullet

analytical methodology, intercalibration

monitoring

pre-1970 references

The remaining file was printed and the articles were found manually in the library where the list was further reduced by deleting non-relevant articles

that were listed in spite of our deletion efforts (see Table 1). Some references were later added manually by incorporating relevant articles found in citations made by the authors of articles originally identified.

Table 1: Computer Assisted Literature Search

	Bio. Abstracts	Aq. Sci. & Fish. Abstracts
Maximum titles found	37,000	53,000
Total titles printed	122	92
Total relevant	16	6

We have accumulated a reference collection totalling 150 titles, including 94 concerning organic pollutants and 56 concerning metals. Although the search did not seek measurements in water and air samples some titles in these areas were found and remain in the collection if they are of regional interest (e.g., whole ocean). Titles which are of relevance to objective 3 are keyed (the key is appended) according to a simplified version of the key used for the biological references. This shortened reference list is the one appended; the longer list containing water and air measurements remains on file.

Reference List Key

Geographic Location

Antarctic, general	ANTR
Arctic	ARCT
Atlantic, north	NATL
Atlantic, south	SATL
Baltic	BALT
Caribbean	CRBN
Indian	INDO
Mediterranean	MDTR
Pacific, north	NPCF
Pacific, south	SPCF

Depth

Surface (< 500 m)	SURF
Midwater	MESO
Bathypelagic	BATH
Benthic	BENT
Depth unknown	DUNK

Taxa

Amphipoda	TxAMP
Aschelminthes	TxASH
Aves	TxAVE
Bivalvia	TxBIV
Carnivora (Seals)	TxCAR
Cephalopoda	TxCEP
Cetacea	TxCET
Chelonia	TxCHL
Copepoda	TxCOP
Crustacea (unspecified)	TxCRU
Decapoda	TxDEC
Echinoidea	TxECH
Elasmobranchii	TxELS
Euphausiacea	TxEUP
Foraminifera	TxFOR
Gastropoda	TxGAS
Heteroptera	TxHET
Holothurians	TxHOL
Isopoda	TxISO
Oligochaeta	TxOLI
Ostracoda	TxOST
Phyceae	TxPHY
Phytoplankton	TxPLK
Polychaeta	TxPOL
Teleosti	TxTEL
Zooplankton	TxZPL

Chemical Registry No.	Chemical Name
T83329	Acenaphthene
T208968	Acenaphthylene
XACENPHEN	Acenaphthylene/Phenanthrene Ratio
T309002	Aldrin
T60571	Aldrin Epoxide
YALKT	Alkalinity, Total
XALKISOP	Alkane/Isoprenoid Ratio
S7429905	Aluminum
S7664417	Ammonia
T120127	Anthracene
S7440360	Antimony
T11097691	Aroclor 1254
S7440382	Arsenic
S7440393	Barium
T56553	Benz(a)anthracene, 1,2-
T50328	Benz(a)pyrene, 3,4-
T71432	Benzene
T58899	Benzene Hexachloride (BHC)
T87854	Benzene, Hexamethyl
YPCB	Biphenyls, Polychlorinated
S7726956	Bromine
T75252	Bromoform
S7440439	Cadmium
S7440702	Calcium
YCPI	Carbon Preference Index
T56235	Carbon Tetrachloride
T7440440	Carbon, Organic
T36884	Carotenoids
T12789036	Chlordane
T479618	Chlorophyll a
S7440473	Chromium
T218019	Chrysene
XCHRYBAN	Chrysene/Benzo(a)anthracene Ratio
S7440484	Cobalt
S7440508	Copper
T360689	Coprostanol
T319846	Cyclohexane, Hexachloro (HCH)
T72548	DDD
T72559	DDE
T50293	DDT (sum)
T53703	Dibenz(a,h)anthracene
T132650	Dibenzo(b,d)thiophene
T132649	Dibenzofuran
T60571	Dieldrin
T1746016	Dioxin
T72208	Endrin
T206440	Fluoranthene

T86737	Fluorene
T86500	Guthion
T76448	Heptachlor
YCH	Hydrocarbons
YHCAL	Hydrocarbons, Aliphatic
YHCALAR	Hydrocarbons, Aliphatic and Aromatic
YHCAR	Hydrocarbons, Aromatic
YHCAROL	Hydrocarbons, Aromatic and Olefinic
YHCDI	Hydrocarbons, Dissolved
YHCOL	Hydrocarbons, Olefinic
YHCSAT	Hydrocarbons, Saturated
YHCUR	Hydrocarbons, Unresolved Complex
YHCUNSAT	Hydrocarbons, Unsaturated
S7553562	Iodine
S7439896	Iron
S7439921	Lead
T58899	Lindane
S7439954	Magnesium
T121755	Malathion
S7439965	Manganese
S7439976	Mercury
T72435	Methoxychlor
S7439987	Molybdenum
T91203	Naphthalene
S7440020	Nickel
S14797650	Nitrite
YNITROGK	Nitrogen, Kjeldahl
T7727379	Nitrogen, Organic
YDO	Oxygen, Dissolved Gas
T56382	Parathion
YPCB	PCB
T12674112	PCB 1016
T53469219	PCB 1242
T11097691	PCB 1254
T11096825	PCB 1260
XPCBDDT	PCB/(Sum of DDT) Ratio
T198550	Perylene
XPH	PH
T85018	Phenanthrene
T108952	Phenol
S7723140	Phosphorus
T84742	Phthalate, Butyl
T117817	Phthalate, Bis-2-ethyl-hexyl
T638368	Phytane
S7440097	Potassium
T1921706	Pristane
XPC17	Pristane/C-17 Ratio
XPC18	Pristane/C-18 Ratio
XPPH	Pristane/Phytane Ratio
T129000	Pyrene
S7702492	Selenium

S7440224	Silver
T111024	Squalene
S7704349	Sulfur
YTSM	Suspended Matter, Total
WTEMP	Temperature
S7440315	Tin
T108883	Toluene
T8001352	Toxaphene (polychlorocamphene)
S7440622	Vanadium
T1330207	Xylene
S7440666	Zinc

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SECTION IIIB. BODY BURDENS OF CONTAMINANTS IN DEEP OCEAN COMMUNITIES

John J. Stegeman

INTRODUCTION

Monooxygenase reactions catalyzed by cytochrome P-450 are instrumental in the oxidative metabolism of many xenobiotics, which in turn are key factors determining both the persistence and effects of organic foreign compounds in the biota. Biotransformation in marine species can result in detoxication, but also activation of many compounds to toxic, mutagenic and carcinogenic derivatives (Stegeman 1981a). The activity of xenobiotic biotransformation enzymes and their regulation could indicate the potential for xenobiotic metabolism and disposition or, conversely, toxication in a given species. Evidence for regulation by environmental chemicals, or induction, could also indicate that certain types of organic compounds are present in a given region at biochemically significant levels.

There is a reasonable literature on energy metabolism and related enzymatic processes in deep-sea animals (e.g., Somero and Siebenaller, 1979; Smith, 1978), but until recently there was no information on processes related to foreign compound metabolism or other interactions with deep-sea fauna. Initial studies on monooxygenase systems were accomplished with samples of six deep benthic fish species, collected in the vicinity of 39°N and 70°W, at depths ranging from about 1400 to 3200 m (Stegeman, 1981b; 1983), a region of the continental slope near the Hudson Canyon. Levels of cytochrome P-450, activities of aryl hydrocarbon hydroxylase, and patterns of benzo[a]pyrene metabolite formation were determined in these fish (Stegeman, 1983). Microsomal systems in some of the animals taken in that area possessed characteristics consistent with the interpretation that hepatic monooxygenase systems had been induced by environmental chemicals that had inductive capacity like 3-methylcholanthrene, or other aromatic

compounds known to be active inducers of cytochrome P-450 in fish. It is possible that those characteristics were associated with constitutive or normally occurring cytochromes P-450, and that the systems merely resembled those of xenobiotic-induced monooxygenases. For a variety of reasons this was considered to be unlikely, but as pointed out earlier (Stegeman, 1983), it was essential to obtain supporting evidence either for or against the possibility of induction. If the results of earlier studies did indicate induction, then it could be presumed to reflect exposure either to biochemically significant levels of anthropogenic compounds, or to natural sediment compounds or other natural products with a capacity to induce cytochrome P-450.

The samples on which the earlier data were obtained could have been exposed to anthropogenic compounds emanating from the eastern seaboard, perhaps associated with sediment transport in the Hudson Canyon. The objectives of the studies reported here were to analyze samples of many of the same species of deep-sea fish examined in the earlier studies, but from similar depths at a site off Newfoundland, quite far removed from the major potential sources of contamination considered proximate to the previous collections. Analysis of polychlorinated biphenyls in a few fish samples from each site revealed sufficient differences in the levels of these residues to suggest that we might be able to discern biochemical differences between animals from the two sites, that might be related to these residues. In this report we describe the results of analysis of that second set of samples and compare these results to those of the first set. Further, we consider these data in relation to the levels of chlorinated hydrocarbon residues, including specific isomers of PCBs which have different biological activities as inducers (e.g., Bandiera et al., 1982). The data presented are relevant in:

1) evaluating the capacity of deep benthic fish for organic compound biotransformation,

2) supporting the indication of induction in previously analyzed samples, and

3) suggesting the nature of the inducers by providing correlation of biotransformation rates with body burdens of contaminants.

Specifically, it had been proposed to provide methods and results of analyses on samples as follows:

I. Samples from OCEANUS-93, near 39°N, 70°W (Site I):

a) ECGC and GC-MS analyses of organochlorines in selected samples (see Farrington).

b) Assay of relevant monooxygenase activities not yet accomplished on these samples.

II. Samples from OCEANUS-126-2, near 45°N, 48°W (Site II):

a) ECGC and GC-MS of organochlorines in selected samples (see Farrington).

b) Levels of microsomal electron-transport components, including cytochrome P-450.

c) Assays of relevant monooxygenase activities, including aryl hydrocarbon hydroxylase, ethoxyresorufin O-deethylase, and possibly aminopyrine N-demethylase and steroid hydroxylase activities.

Due to limitations of sample volume not all analyses could be accomplished. However, the studies that were done, including some additional to the ones proposed, allow for substantive conclusions concerning contamination and biochemical effects in the deep sea.

MATERIALS AND METHODS

Chemicals

7,8-benzoflavone (α-naphthoflavone; ANF) was obtained from Aldrich Chemical Company, Milwaukee, WI [^{3}H]-benzo[a]pyrene (BP) was obtained from Amersham Inc. Arlington Heights, IL, and was purified as in Binder and Stegeman (1981). Resorufin was obtained from MCB Chemical Company and 7-ethoxyresorufin (ER) was synthesized according to the methods of Prough et al. (1978). 8-^{14}C-styrene oxide was obtained from Amersham, Inc., Arlington Heights, IL. Ethoxycoumarin was obtained from Aldrich Chem. Co. Reduced nicotinamide adenine dinucleotide phosphate (NADPH)

and NADH were obtained from the Sigma Chemical Co., St. Louis, MO. Materials for high pressure liquid chromatography (HPLC) were obtained from Burdick and Jackson, Muskegon, MI, and from DuPont, Wilmington, DE.

Animals

Deep benthic species were obtained by trawling with a 12.5 m Gulf of Mexico shrimp trawl on the R/V OCEANUS in the vicinity of 39°N, 70°W and in the vicinity of 45°N, 49°W (Figure 1), from various depths (Table 1). Animals of several species (Table 2) were retrieved through cold waters (surface temperatures near 6°C) and were dissected within minutes after reaching the deck. All animals had some minimal signs of life (beating heart). The sizes of some, e.g., C. armatus, were small enough to suggest that these were juvenile fish, and gonads of the animals were not obviously developed. Livers were removed from the animals usually within 15 min of arriving on deck, were immediately frozen in liquid N_2, and then stored at -80°C until microsomes were prepared ashore, within 8 days after freezing.

Tissue Preparation

All procedures were carried out at ice temperature. Livers of deep-sea species were thawed to ice temperature, tissues were finely minced and homogenized in 5 vol of 50 mmol potassium phosphate/L, pH 7.4, containing 1.15% KCl. Subcellular fractionation was accomplished as previously described (Stegeman, 1983), except that some samples were recentrifuged as before (Stegeman, 1983) to aid in removing lipid. Microsomal fractions were resuspended in 50 mmol Tris/L containing 1 mmol EDTA/L, 1 mmol dithiothreitol/L and 20% glycerol by volume. Preparations were used directly or were archived in liquid nitrogen until use.

Enzyme Assays

All enzyme assays were carried out at 20°C, determined to be optimal for activity in these species. Activity of benzo[a]pyrene hydroxylase, was assayed radiometrically (see Stegeman et al., 1981). Final reaction volumes of 50 ul consisting of approximately 50 ug of microsomal protein,

50 mM Tris pH 7.4, 1.2 mM NADPH, and 62 uM benzo[a]pyrene (specific activity = 227 uCI/umole), with or without 100 uM of the competitive inhibitor -naphthoflavone, were incubated for 20 min at 20°C. Blanks contained boiled enzyme. Reactions were stopped by the addition of 250 ul of a mixture of 4 parts 85% DMSO/0.15 N KOH with 1 part Tris buffer. Unmetabolized substrate was extracted with 2 X 0.75 ml hexane. 100 ul aliquots of the extracted aqueous layer were counted in 3 ml Scintil Verse II to which 20 ul of 0.6 N HCl had been added. All procedures were conducted under red light to prevent photooxidation of the substrate.

7-ethoxyresorufin O-deethylase (EROD) activity was measured spectrophotometrically at 572 nm using the reported extinction coefficient of 73 mM^{-1} cm^{-1} (Klotz et al., 1984). Reaction mixtures containing 20 to 75 pmoles of microsomal cytochrome P-450 in 0.1 M Tris buffer pH 8.0, 0.1 M NaCl, and 2 uM 7-ER were initiated by the addition of NADPH to a final concentration of 500 uM. Reactions were linear for at least 3 min at 18-20°C.

7-ethoxycoumarin O-deethylase (ECOD) activity was determined spectrofluorometrically. Approximately 20 pmoles of microsomal P-450 were incubated with 0.4 mM 7-EC and 0.5 mM NADPH in a 100 ul reaction mixture, which was kept at 20°C and stopped after 20 min with 0.6 parts 2 N HCl and 3.4 parts Tris buffer. The product was extracted with 900 ul $CHCl_3$, and 600 ul added to 3 ml of 30 mM $Na_2B_4O_2$ at pH 9.2. Fluorescence was read, subtracting boiled blanks, with an emission wavelength of 455 nm and an excitation wavelength of 370 nm, against a standard curve of hydroxycoumarin, the deethylation product formed in the assay.

Metabolites of α-naphthoflavone were produced in 1.0 ml reaction mixtures as previously described (Stegeman and Woodin, 1980), that contained about 0.3 mg microsomal protein. Reactions were incubated at 20°-25°C for 20 minutes, stopped, extracted and analyzed by HPLC as previously described (Stegeman and Woodin, 1980).

Epoxide hydrolase activity was determined radiometrically with 8-^{14}C-styrene oxide (James et al., 1979, and personal communication). The substrate was purified by hexane extraction, with 80% of the

substrate partitioning into the solvent, and diluted with cold styrene oxide to a specific activity of 0.526 uCi/umole. A final assay volume of 150 ul contained 100 ug of protein in 25 mM Tris, 0.03% Tween 80, pH 8.7, and the initiating substrate at a concentration of 0.1 mM, at 30°C. Reactions were stopped by the addition of 3 ml hexanes and vortexing, and unreacted styrene oxide was extracted 3 times with hexanes. Test tubes were placed in a dry ice acetone mixture for 60 sec, freezing the aqueous layer and allowing complete removal of the solvent. The styrene glycol product was extracted from the remaining aqueous with 2X 2 ml of ethyl acetate. Zero time blanks were measured by addition of the hexanes prior to initiation of the reaction with substrate.

Levels of NADH-cytochrome c (b_5) reductase and NADPH-cytochrome c (P-450) reductase activity had been measured previously as described (Stegeman et al., 1981) in both sets of deep sea samples. These assays were repeated with both sets of samples.

Cytochrome P-450 and cytochrome b_5 content were measured using a Cary 118C dual beam spectrophotometer. Microsomes were diluted in resuspension buffer to a final volume of 1.2 ml containing between 0.74 and 1.52 mg protein per ml. Diluted microsomes were divided equally between sample and reference cuvettes and a continuous baseline difference spectrum was determined from 500 to 400 nm. NADH was added to the sample cuvette to a final concentration of 58 uM, and the resulting difference spectrum was used to determine the amount of cytochrome b_5 present, as described previously. Samples were withdrawn, mixed, further reduced with NADH, bubbled with CO, divided between sample and reference cuvette and sample was reduced with $N_2S_2O_4$ for analysis of cytochrome P-450.

Protein content was determined according to Lowry (1951), with BSA used as a standard. Limits of detection for the various assays were as previously described (Stegeman, 1983).

Microsomal proteins (and appropriate molecular weight standards) from C. armatus were separated on a 9% acrylamide gel with sodium dodecyl sulfate (SDS), prepared as described previously (Stegeman et al., 1981).

RESULTS

Many of the data obtained for deep sea fish caught in the region of the Hudson Canyon (Site I) have been reported (Stegeman, 1983) and are included here to provide essential comparison with the more recent data on the same species from Site II. Some data from Site I animals are, however, novel contributions in this report, or represent a re-analysis of archived samples from Site I, repeated to verify original results and provide consistency in analytical methods.

The levels of microsomal protein and cytochromes P-450 and b_5 are essentially the same within species from the two sites (Table 3). The similarities are evident particularly within C. armatus and A. rostrata. The levels of cytochrome P-450 were highest in C. armatus from both sites, which species also had the highest microsomal yield. The values for C. rupestris from Site II were like the value for the single specimen from Site I. The comparatively low levels of cytochrome P-450 in A. rostrata, and to some extent in C. rupestris, presumably reflect the presence in these samples of cytochrome P-420, a chromophore generally identified with denatured cytochrome P-450. The levels of cytochrome P-420 were particularly high in A. rostrata, representing nearly 3 times the amount of native P-450, a circumstance that was seen in samples of this species from both Site I and Site II. Cytochrome P-420 was either absent or insufficient for quantification in C. armatus at either site. The presence of such abundant P-420 in A. rostrata presumably reflects some inherent sensitivity of P-450 in this species to destabilizing factors associated with retrieval from depth. Attempts to limit the formation of cytochrome P-420, by lowering the assay temperature or allowing more extensive time for reduction were not successful. The levels of NADPH- and NADH-cytochrome c reductase activities were generally the same at both sites or were slightly higher in the samples from Site II which, if anything, might suggest that there had been less degradation or loss of these microsomal components than might have occurred in samples previously analyzed.

These data indicate the suitability of C. armatus microsomes for analysis of catalytic function in xenobiotic metabolism. On the other

hand, data for C. rupestris and A. rostrata, particularly the evidence for instability or degradation of the catalyst P-450, render these species less suited to some comparative studies. However, data for these species are included as they constitute a unique basis of comparison for any future studies. Furthermore, some interpretations can be made from data normalized to cytochrome P-450, which should reveal the catalytic efficiency of the native P-450 remaining, and not be influenced by denatured forms. However, the discussion will center on C. armatus.

The activities of AHH and EROD expressed per mg protein (Table 4) in C. armatus were substantially (5 to 7 fold) lower in animals from Site II than in those from Site I. The lower AHH activity was associated with a lower sensitivity of this activity to ANF inhibition, which averaged 95% inhibition at Site I but only 20% or less at Site II. By contrast, the activity with ethoxycoumarin was the same between these two groups. The pattern seen in activities normalized to protein was also seen in activities normalized to P-450 (Table 5). This latter measure indicates that the catalytic efficiency of the native P-450 present for both AHH and EROD was greater, again by 6-9 fold, in the animals from Site I than from Site II. Such a pattern of activity is consistent with the presence of hydrocarbon-induced microsomal cytochromes P-450 at Site I, by comparison with experimentally induced and control microsomes in several other fish species. This same pattern was not seen for ECOD which, although catalyzed in part by P-450 induced by hydrocarbon-type inducers, is also catalyzed substantially by other isozymes of cytochrome P-450. The above pattern in AHH activity normalized to P-450 found in C. armatus was not seen in A. rostrata, in which the native P-450 present was catalytically similar in animals at the two sites. However, excluding the contribution of one high value disclosed a trend to lower turnover number in EROD activity in A. rostrata from Site II.

Patterns of flavonoid metabolism analyzed in other fish species have indicated a regiospecificity, with certain metabolites being produced preferentially by MC-induced isozymes of P-450 (Stegeman et al., 1984a). The in vitro metabolites of α-naphthoflavone formed by microsomes from C. armatus at Site I (as shown in Figure 2) include a peak coeluting with

ANF-7,8-dihydrodiol that was the major metabolite, like the major metabolite produced by MC-induced trout. The nature of activity in these microsomes was further indicated by the inhibition of AHH activity by antibodies specific to the major hydrocarbon-induced isozyme of cytochrome P-450, and the major AHH catalyst, from the marine teleost scup (Klotz et al., 1983). These antibodies are specific for the induced P-450 in scup, yet apparently cross-react with the induced catalysts from other teleost species (Stegeman et al., 1984, unpublished information), and inhibition here indicates further the presence of an induced enzyme in C. armatus from Site I.

Analysis of microsomal protein from C. armatus from the two sites by SDS-polyacrylamide gel electrophoresis revealed that bands in the P-450 molecular weight range (49,000 to 57,000 daltons) differed between the two sites at the region near 55,000 daltons, as indicated in Figure 3. The lower member of a doublet at this region, which is the molecular weight range characteristic of hydrocarbon-induced P-450s, was more pronounced in the fish from Site I. There was also a correlation with AHH activity at Site I, and the individual with the highest AHH activity was also the one with the most pronounced lower band in the doublet at this position.

Levels of epoxide hydrolase in liver microsomes from C. armatus were assayed to estimate the capacity for epoxide metabolism. Purification of the radiolabeled substrate styrene oxide was necessary due to high backgrounds initially recorded, allowed the measurement of pools (each consisting of two individuals) of C. armatus from Site I and from Site II. Fish from the first area had an average activity of 0.75 nmol/min-mg, and those from the latter had an average activity of 1.79 nmole/min-mg, both of which are within the range found in fish, although toward the low end of this range (James et al., 1979). Further analyses, particularly the effects of the addition of epoxide hydrolase on benzo[a]pyrene metabolite profiles or the inclusion of known inhibitors of EH will prove interesting.

The above results describe a signature of cytochrome P-450 induction by environmental chemicals in fish (C. armatus) from Site I. The

Possibility that this might be linked to environmental chemicals was strongly supported by the analysis of chlorinated hydrocarbon residues in liver of fish from the two sites (Table 6), which describes a level of PCBs in animals from Site I, that was was nearly 7 times the level present in liver at Site II. Moreover, the absolute levels seen. 4,5 ug/g, are like those known to elicit strong induction of cytochrome P-450 in some other fish (e.g., Binder et al., 1985).

DISCUSSION

In a previous study of deep sea fish (Stegeman, 1983) we established that it was possible to retrieve deep benthic species from depth and obtain liver microsomal preparations that were suitable for analysis of monooxygenase systems. Further, the results of that study indicated species differences in the apparent stability of cytochromes P-450 during retrieval, archiving and/or membrane preparation, with the systems in C. armatus being highly stable, those in A. rostrata being very unstable, and those in several other species having intermediate stability, as judged from the content of cytochrome P-420 in microsomal preparations. Analysis of the samples from Site II has provided results that closely paralleled those from Site I, thereby confirming these observations regarding retrieval of deep sea fish and the appearance of species differences in the characteristics of hepatic microsomes.

A speculation in that earlier study, that cytochrome P-450 in C. armatus near the Hudson Canyon had been induced by environmental chemicals, was based on the evidence of specific activity and turnover numbers for both AHH and EROD activity, and the inhibition of AHH activity by ANF, all of which resembled the characteristics present in other teleost fish known to be experimentally induced. The conclusion that these earlier results indicated induction were considerably strengthened by the findings presented here that C. armatus from near the Hudson Canyon had additional catalytic features, including formation of the 7,8-dihydrodiol of ANF, a prominent metabolite of hydrocarbon-induced P-450 in other teleosts, and that monooxygenase activity in these animals was inhibited by antibodies against hydrocarbon-induced cytochrome P-450

from another teleost. That both EROD and AHH activity were an order of magnitude lower in hepatic microsomes of C. armatus from a second, distant site, while the levels of microsomal electron transport components and an additional P-450 catalytic function were the same between the two sites, lends even further substance to the conclusion that C. armatus from Site I were induced. The appearance of electrophoretic distinctions is further consistent with this conclusion and suggests a molecular weight near 55 Kd for the induced protein.

The origin of apparent induction is a matter of some concern in this study, as in other studies of this phenomenon in feral populations (e.g., Stegeman et al., 1981; Foureman et al., 1983). Biological differences between animals at Site I and Site II are not likely to contribute greatly to the differences in monooxygenase activity. Electrophoretic analysis of 27 presumptive loci in C. armatus sampled at Site I on the same cruise as the animals described here, and from a site in the North Pacific, revealed an unexpectedly high degree of genetic similarity (Wilson and Waples, 1984). This would suggest little genetic difference might occur between the animals from separate locations here. Furthermore, the animals analyzed were of a similar size and had undeveloped gonads, ruling out developmental or reproductive differences. In the present study, the finding of pronounced difference in the levels of polychlorinated biphenyls, known to include isomers which are hydrocarbon or MC-type inducers that are active in fish, suggests that these compounds could be responsible for the apparent induction, although further consideration of the other organochlorine compounds present in these animals (see Farrington) is warranted. Tentatively, the clear presence of characteristics that constitute a signature of induced cytochrome P-450 in C. armatus from near the Hudson Canyon, but not near the Carson Canyon, and the correlation with PCB residues clearly implicates these compounds in the appearance of induction.

Contaminants in the sediment are considered to be the likely source for the bulk of the residues in fish from the Hudson Canyon. Accumulation of hydrocarbons from sediment is known in fish, but whether

direct transport or transport via contaminated benthos serving as food might be the dominant vector in this case is not known. The possibility that some C. armatus might acquire a different residue burden by swimming up to feed in the midwater, as some larger C. armatus in the Hudson Canyon do (Haedrich and Henderson, 1974), rather than feeding in the sediment as these fish can do (McClellan, 1977), is not likely to contribute to any differences here. Animals from both sites were of a similar size, and smaller than those which have been found to make excursions into the midwater. Mauchline and Gordon (1984) noted that the C. armatus fed principally on organisms in the water column immediately above the sea bed in another region (Rockall Trough) and that there was not a strong ontogenic distinction in feeding off the bottom as seen by Haedrich and Henderson (1974).

The results here provide the first clear example indicating a biochemical effect of organic contaminants in the deep sea, but the consequences of this effect are not known. Induction of monooxygenases is principally an adaptive mechanism, promoting more rapid metabolism and elimination of organic compounds. However, metabolism can at the same time activate many such compounds, including carcinogens, to electrophiles that can bind to various cellular macromolecules. Furthermore, the potential exists for induction to alter the rate of metabolism of important biological molecules, including steroid hormones, or to alter the amount and identity of foreign compounds that are transported to and deposited in the gonads during gametogenesis. These and other questions, including the role of these processes in contributing to the transformation of organic compounds in seawater, the metabolism of PCB isomers in the deep sea, the patterns of steroid metabolism, the effects of pressure on the catalytic function of P-450 in the deep sea, and the evaluation of foreign compound metabolism in additional deep sea species, require attention before the significance of cytochrome P-450 function and its induction in the deep sea can be fully appreciated.

In summary, the data presented here on monooxygenase systems in deep sea fish from two sites in the Western North Atlantic constitute a basis

for comparison with any future studies of xenobiotic metabolism in deep-sea fauna. The results provide a relative measure of the capacity of deep benthic fish to metabolize foreign organic compounds, and provide direct information on the question of whether species in some deep-sea communities are presently suffering effects of exposure to biochemically significant levels of certain classes of organic compounds. The focus in this research was on fish, but the results suggests it should be possible to estimate the nature of effects in some invertebrates. The results further suggest that biochemical surveys in particular areas of the world's deep ocean could reveal effects there, and may, because of the link between biotransformation, organ toxicity and/or carcinogen activation, suggest where surveys of fish for pathologies, perhaps including gonadal dysfunction, might be warranted.

Regarding comparison between deep sea and coastal species, a strict comparison of sensitivity of induction response between coastal and deep sea species cannot be made, given the present inability to execute appropriate experiments in the deep sea. Furthermore, there are very few explicit dose response studies that relate monooxygenase induction to dose as measured in an individual or organ, rather than doses administered. However, in studies with Fundulus heteroclitus (Binder et al., 1985), we have found that maximal induction can occur at a body concentration of less than 10 ug PCB (Aroclor 1254) per g wet weight, and that significant induction can occur at concentrations as low as 1 ug per g. Although the distribution of PCBs measured in the liver of fish here could include substantial fractions present in abundant lipid vacuoles in hepatocytes, it seems clear that the organ contents estimated at 2 to 10 ug/g liver could be expected to elicit a rather significant induction. The levels of PCBs in many coastal fishes might also be expected to produce induction, though the links between the compounds and the extent of induction have not been made. Given only the levels of PCBs measured in the C. armatus by Farrington, and the knowledge of dose-response in Fundulus (Binder et al., 1985), we would have suspected a lesser degree of induction in the C. armatus from Newfoundland.

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RECOMMENDATIONS:

In addition to the lines of study suggested in the text, the following recommendations might be made:

1. Additional analyses of body burdens of organic contaminants in species having different feeding strategies and life histories should be carried out in conjunction with studies on biotransformation systems in these species. Such studies should include analysis of biliary metabolites.

2. Studies should be carried out to evaluate the significance of hydrostatic pressure to the function of biotransformation enzymes in deep sea animals.

3. Relationships between steroid metabolism and xenobiotic metabolism should be evaluated.

4. The potential for metabolism of specific compounds, e.g., specific PCB isomers, that are prominent contaminants should be evaluated.

5. The geographic range of apparent induction in the deep sea can, at least in Coryphaenoides armatus, now be assessed, and should be.

6. There should be thought given to an experiment in situ, with the objective of experimentally verifying induction in deep-sea fish.

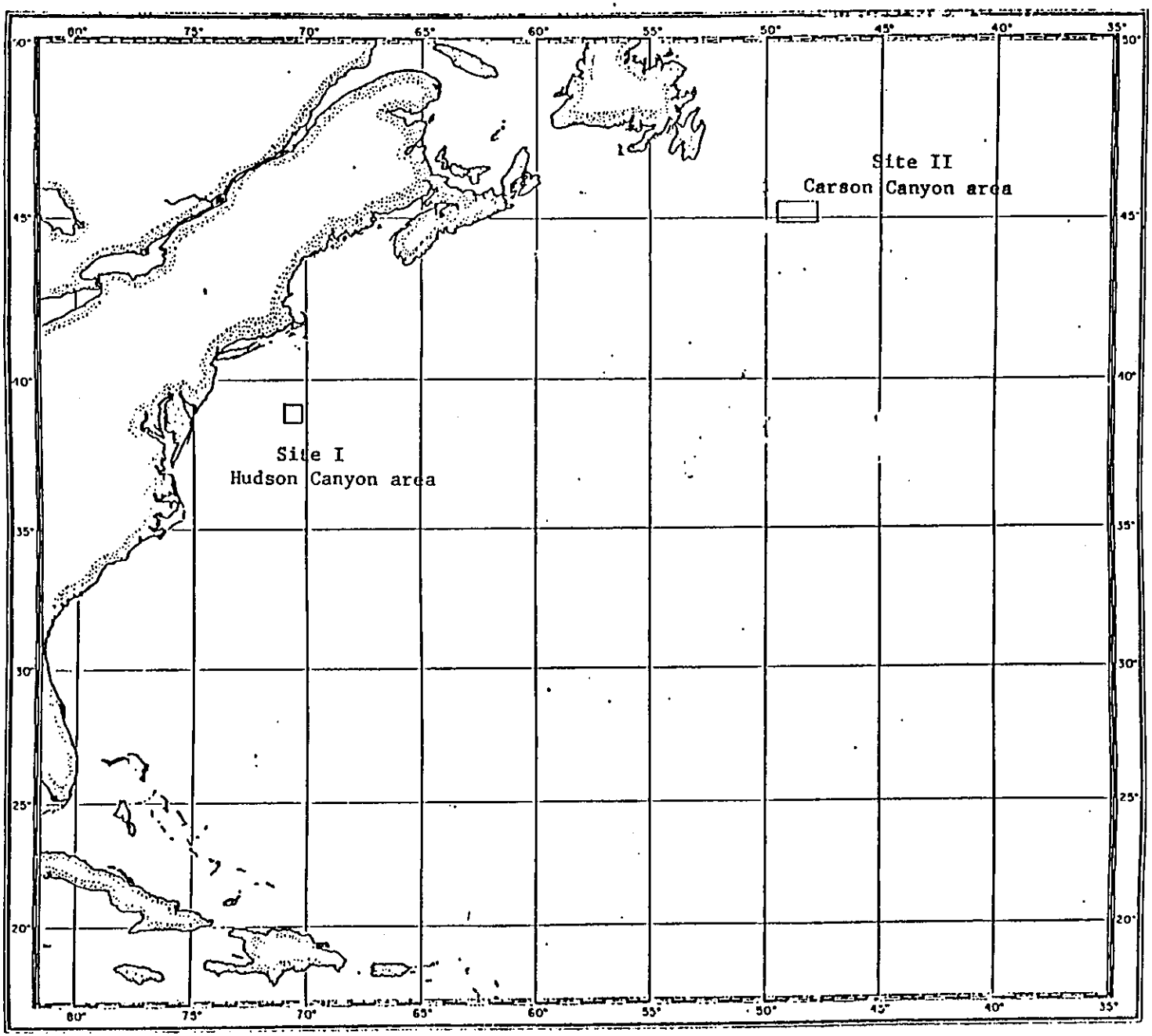
FIGURE LEGENDS

Figure 1. Location of sampling sites. Site I was located near 39°N, 70°W, on the continental slope in the vicinity of the Hudson Canyon. Site II was located near 45°N, 49°W on the slope of the Grand Banks near the Carson Canyon area.

Figure 2. High pressure liquid chromatogram of α-naphthoflavone metabolites produced by C. armatus liver. Conditions for assay are as described in Materials and Methods. A. Blank reaction, minus NADPH. B. Complete reaction, plus NADPH. ANF; α-naphthoflavone. Peak at the 7,8-dihydrodiol, was identified by retention time and mass spectral analysis. Peak b is an unknown phenolic derivative.

Figure 3. SDS-polyacrylamide gel electrophoresis of C. armatus liver microsomes. Conditions for electrophoresis are as described in the Materials and Methods. 1-4, samples from Site I. 5-8, samples from Site II. Sample 2 had the highest AHH activity. S, molecular weight standards. Arrow indicates region of interest.

FIGURE 1.


80°
75°
70°
65°
60°
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50°
45°
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Site I
Hudson Canyon area
Site II
Carson Canyon area

Figure 2

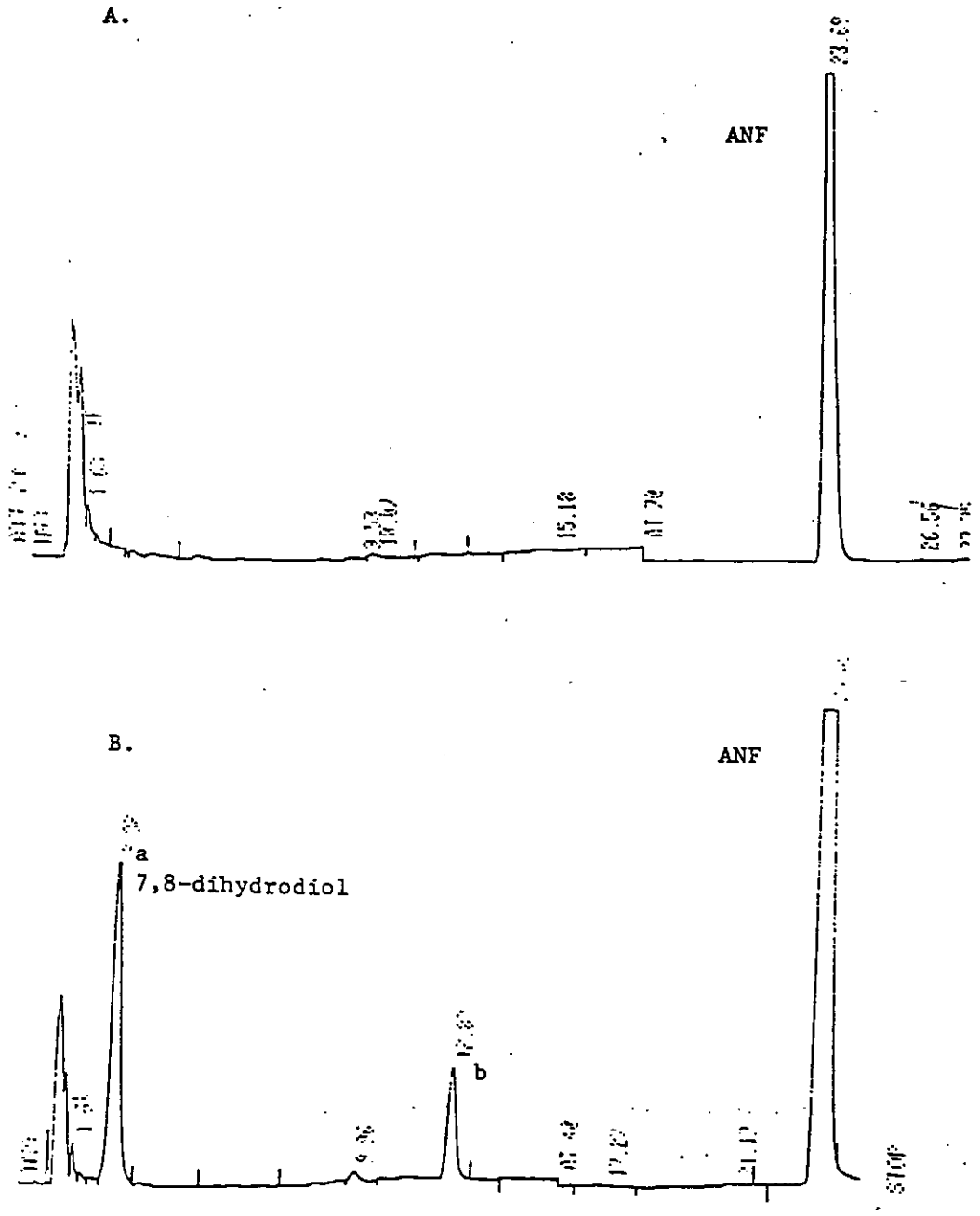

Figure 3

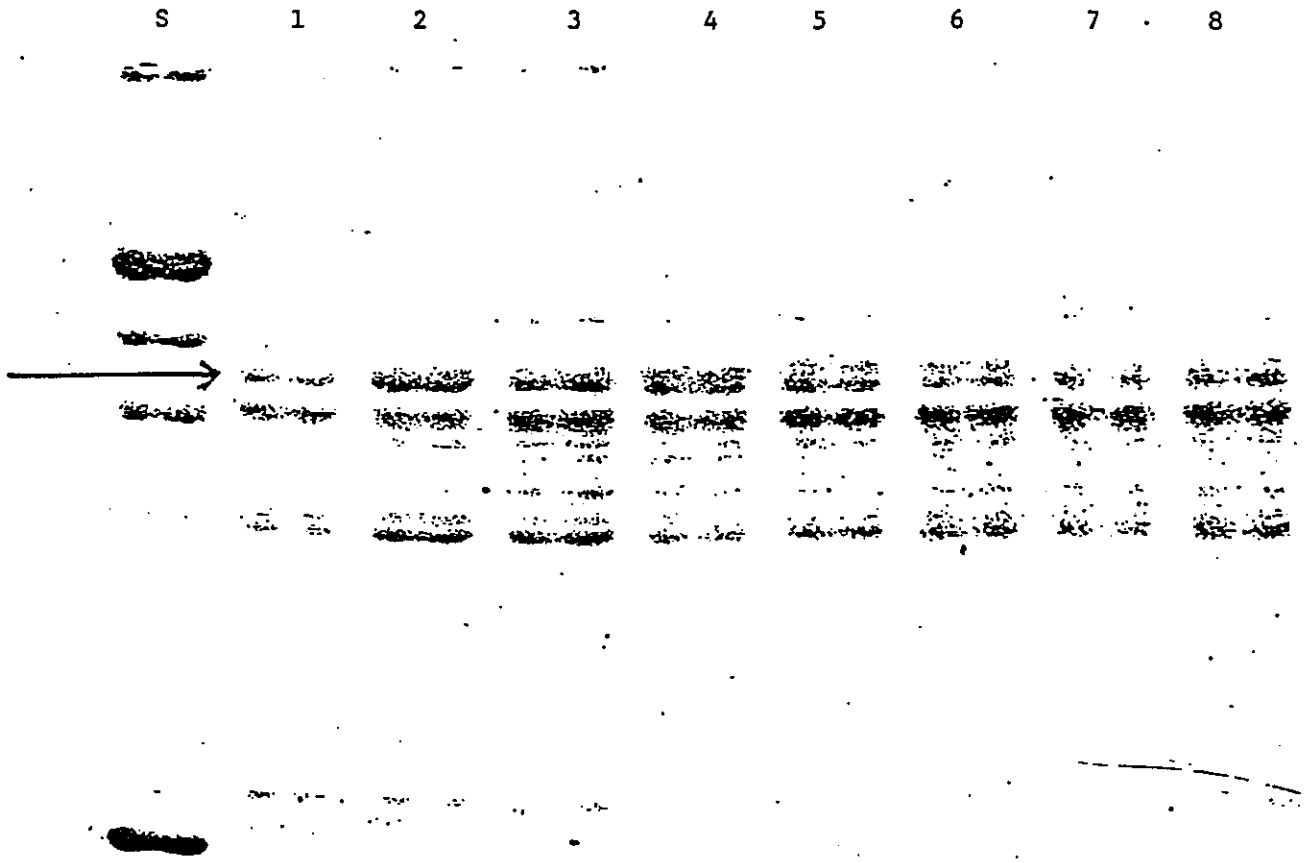

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Table 1. Trawl Data.

Site	R/V OCEANUS Cruise No.	Trawl No.	Date	Location [a] North	Location [a] West	Depth[b] (m)
I	93	900	28-3-81	38°35'	69°58'	3245
		903	29-3-81	39°48'	69°45'	1410
II	126-2	1352	11-9-82	45°18'	48°35'	1300
		1354	12-9-82	45°21'	47°43'	2300
		1359	13-9-82	45°33'	47°36'	1700
		1360	13-9-82	45°33'	47°30'	1850
		1363	14-9-82	45°17'	48°34'	1200

[a]Location of ship as trawl was set.

[b]Average depth of trawl.

Table 2. Fish sampled at Sites I and II.

Species	Site	Trawl	Depth (m)	N Fish	Size or weight[a] (g)	Condition[b]	Minutes to Freezing[c]
C. armatus	I	900	3245	4	44±20	alive	15
	II	1354	2300	6	61±22	alive	20
		1359	1700	2	41±16	alive	30
C. rupestris	I	903	1410	1	65	alive	15
	II	1352	1300	1	104	alive	20
		1363	1200	4	124±50	alive	20
A. rostrata	I	903	1410	5	167±91	alive	15
	II	1359	1700	4	220±20	moribund	30
		1360	1850	4	400±100	alive	15

[a]Size (length) was measured and weight was inferred based on liver weight/body weight ratios previously determined for these species. These were 0.072±0.037 (N = 10), for C. armatus and 0.03 to 0.60 for A. rostrata of sizes similar to those seen here. Length estimates for A. rostrata were 40-50 cm for animals at Site II. The liver weight/body weight ratio used for C. rupestris, 0.110, was an average of values obtained for 15 specimens in 3 species of Coryphaenoides, but not in C. rupestris, for which data are not available.

[b]Fish were judged to be alive when the heart was beating upon dissection, however, some fish showed signs of activity as well.

[c]Time elapsed between arrival of net on deck and the freezing of liver in liquid N_2.

Table 3. Hepatic microsomal electron transport components in deep benthic fish from two sites.[a]

Sample	(N)	Microsomal yield (mg/g)[a]	Cytochrome P-450 (nmol/mg)[b,e]	Cytochrome b_5 (nmol/mg)[b]	Cytochrome c Reductase NADPH (nmol/min/mg)[c]	Cytochrome c Reductase NADH (nmol/min/mg)[c]
C. armatus						
Site I	(4)	9.4±3.4[d]	0.251±0.069	0.040±0.023	89± 6	32±15
Site II	(6)	11.0±2.5	0.321±0.043	0.052±0.023	90±28	137±76
C. rupestris						
Site I	(1)	2.5	0.080	0.010	35	100
Site II	(5)	3.6±0.4	0.124±0.03	0.026±0.018	82±15	346±38
A. rostrata						
Site I	(5)	6.5±3.5	0.083±0.018	0.017±0.014	55±11	105±41
Site II	(8)	5.8±2.1	0.082±0.041	0.021±0.011	31±7	118±27

[a]nmol microsomal protein per g liver.

[b]nmol per mg protein.

[c]nmol cytochrome c reduced per min per mg protein. The values appearing for NADPH cytochrome c reductase activity at Site I were obtained by re-analysis of samples at the same time samples from Site II were analyzed.

[d]Values are means ± standard deviation. All data for Site I are from Stegeman, 1983.

[e]The levels of cytochrome P-420 estimated in *C. rupestris* and *A. rostrata* averaged 0.04 ± 0.03 nmol/mg and 0.46 ± 0.28 nmol/mg, respectively, regardless of site.

Table 4. Monooxygenase specific activity in hepatic microsomes from deep sea fish.

Sample	Aryl hydrocarbon hydroxylase (nmol/min/mg)	Ethoxyresorufin O-deethylase (nmol/min/mg)	Ethoxycoumarin O-deethylase (nmol/min/mg)
C. armatus			
Site I	0.109 ± 0.067[a]	0.285 ± 0.123	0.039 ± 0.038
Site II	0.015 ± 0.012	0.060 ± 0.056	0.031 ± 0.009
C. rupestris			
Site I	0.002	0.021	-
Site II	0.004 ± 0.002	0.041 ± 0.018	0.137 ± 0.055
A. rostrata			
Site I	0.003 ± 0.002	0.056 ± 0.019	0.023 ± 0.012
Site II	0.010 ± 0.019[b]	0.040 ± 0.047[b]	0.048 ± 0.026

[a]Values are all nmoles produced per min per mg microsomal protein, and are means ± one standard deviation.

[b]High variability is due principally to the contribution of one animal with a comparatively high activity for AHH and for EROD activity. Without this sample, values (N = 7) were 0.003 ± 0.003 and 0.024 ± 0.014 for AHH, and EROD, respectively.

Table 5. Catalytic efficiency of hepatic microsomal cytochrome P-450 in deep sea fish.

	Aryl Hydrocarbon Hydroxylase (nmol/min/nmol P-450)	Ethoxyresorufin O-deethylase (nmol/min/nmol P-450)	Ethoxycoumarin O-deethylase (nmol/min/nmol P-450)
C. armatus			
Site I	0.408 ± 0.340[a]	1.175 ± 0.617	0.164 ± 0.154
Site II	0.045 ± 0.030	0.198 ± 0.137	0.097 ± 0.020
C. rupestris			
Site I	0.02	0.149	-
Site II	0.038 ± 0.021	0.329 ± 0.152	1.09 ± 0.36
A. rostrata			
Site I	0.035 ± 0.020	0.720 ± 0.310	0.303 ± 0.188
Site II	0.100 ± 0.140[b]	0.491 ± 0.350[b]	0.569 ± 0.291

[a]Values are nmoles product per minute per nanomole of native P-450 measured, and are means ± one standard deviation.

[b]High variability is due principally to the contribution of one animal with a comparatively high activity for AHH and for EROD activity. Without the high value the means ± S.D. (N = 7) were 0.048 ± 0.037 and 0.386 ± 0.197 for AHH, and EROD, respectively.

Table 6. Chlorinated hydrocarbon residues in liver of *Coryphaenoides armatus*.

Sample Location	Σ DDE	Σ Aroclor (1242 + 1254 + 1268) Equivalents
Site I	2.1 ± 0.41*	4.49 ± 1.99
Site II	.27 ± .151	.76 ± .547

[a]Values are all in 10^{-6} per g wet weight (parts per million) and are averages of five separate livers (Site I). and two separate livers (Site II).